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TESTING THE ECOMORPHOLOGICAL PARADIGM IN JUVENILE ATLANTIC SALMON (*SALMO SALAR*)

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RESUME

L'ecomorphologie étudie les interactions entre la morphologie des organismes et leur écologie. La variation morphologique peut influencer la performance des individus au sein d'une population et avoir des conséquences sur leur survie. Bien que certains de ces traits soient héritables et produisent des différences entre les individus, ceux-ci varient tout au long de la vie des individus. L'hétérogénéité des habitats, les interactions entre espèces et les différences de comportement entre individus peuvent influer sur la relation entre morphologie, performance et survie. Cependant, la nature de ces interactions reste ambiguë et l'impact de la compétition inter et intraspécifique sur la variation morphologique des individus, par exemple, est toujours méconnu. Ces questions sont non seulement intéressantes du point de vue théorique; elles ont également des applications pratiques. Les programmes de gestion et de conservation des populations ont besoin de données empiriques afin de les guider dans leurs décisions. En ce sens, le but de cette thèse est l'étude des interactions entre la variation morphologique, l'hétérogénéité des habitats, la compétition inter et intraspécifique et le comportement individuel, et de leur impact sur un trait important pour la survie : la croissance. Pour atteindre cet objectif, je me suis servi de deux populations de saumons atlantiques juvéniles comme organismes modèles. Le saumon atlantique est une espèce importante sur les plans économique et écologique, et sont connus pour leur plasticité morphologique et comportementale durant leur développement. Comprendre la complexité des interactions entre ces différents éléments est essentiel au succès des programmes de réintroduction. Cette thèse se divise en quatre chapitres qui proposent d'étudier différents aspects de ces relations. Le chapitre 1 explore la relation entre la morphologie et la performance de nage. La manière dont la morphologie influence la dispersion des individus dans l'environnement est également abordée. Le chapitre 2 propose de tester si la compétition interspécifique peut avoir un impact négatif sur la morphologie et la performance des individus. Le chapitre 3 propose de tester l'effet de l'environnement biotique et abiotique sur la variation morphologique et la croissance. Enfin, le chapitre 4 va plus loin que le chapitre 3 en évaluant comment l'effet du comportement individuel peut mener à des différences morphologiques et de croissance dans différents environnements. Cette thèse porte sur, et contribue à, l'ecomorphologie et l'écologie comportementale en établissant des liens jusqu'ici absents de la littérature scientifique. De plus, cette thèse peut servir d'outil de conservation, non seulement pour le saumon atlantique ou d'autres poissons, mais aussi en tant que cadre général applicable à plusieurs taxons d'espèces.

Mots-clés : Ecomorphologie, écologie comportementale, saumon atlantique, geomorphometrics, performance, personnalité, plasticité phénotypique, choix de microhabitat

SUMMARY

The goal of ecomorphology is to understand the interactions between the morphology of organisms and their ecology. Variation in morphology can directly influence organismal performance which will produce differences in fitness among individuals in a population. While certain elements of morphological variation are heritable and result in intra-specific variation for a given trait, morphological traits can also be highly plastic in individuals over the course of their lives. Habitat heterogeneity, interspecific interactions and individual differences in behaviour have all been shown to influence the causal relationships between morphology, performance and fitness; however, the nature of many of these relationships is still unclear. Among them, it is still largely unknown how inter and intraspecific competition modulates variation in morphology and how these interactions act across heterogeneous environments to generate differences in fitness. These questions are not only interesting from a theoretical stance but have practical applications as well. Conservation management and reintroduction programs need empirical data to show how these elements can interact and contribute to individual survival and successful population management. To this end, the goal of this thesis was to study the interactions between morphological variation, habitat heterogeneity, inter and intraspecific competition, and how they impact individual performance and are modulated by individual variation in behavioural traits to influence a fitness-related trait: growth. To accomplish this, I used populations of juvenile Atlantic salmon (*Salmo salar*) as a model organism. They are an important species ecologically and economically and are known to be highly plastic in many of their morphological and behavioural traits during their early lives. Understanding the variability and phenotypic plasticity in their traits is instrumental to the success of fish reintroduction programs. This thesis is composed of four chapters that are experimental in nature and whose goal is to account for individual variation and establish links between the aforementioned traits. Chapter 1 investigated how individual variation in morphology influenced swimming performance and whether morphology constrained habitat choice and could be used to predict habitat preference among a diverse set of microhabitat features in natural streams. Chapter 2 investigated how competition with non-native interspecific competitor salmonids impacted morphology and swimming performance. Chapter 3 examined how an interaction between the abiotic and biotic environment influenced intraspecific competition and lead to differences in morphology and growth. Finally, Chapter 4 expanded upon Chapter 3's scope and evaluated how plasticity in behaviour, as well as different personalities in individuals, influenced morphology and growth in a heterogeneous environment. This thesis contributes to ecomorphology and behavioural ecology theory, establishing relevant and previously

undocumented relationships between morphology, performance, behaviour, competition, and how they contribute to individual growth. This thesis also serves as a tool for conservation authorities and fisheries, not only for the Atlantic salmon or salmonids and other fishes but as a general framework applicable across a large range of taxa.

Keywords: Ecomorphology, behaviour ecology, Atlantic salmon, geomorphometrics, whole organism performance, personality, phenotypic plasticity, microhabitat choice

INTRODUCTION

0.1 Individual variation and ecomorphology

Ecological and evolutionary theory rests on the fact that individuals vary (Darwin 1859). Despite the common practice to treat the variation of traits within populations or even within individuals as noise around the mean (Westneat et al. 2014), variation in the morphology, behaviour, and other life-history traits of individuals can be major drivers of evolution and are at the heart of many observable ecological processes. Natural selection can act directly on these phenotypes regardless of the genotype and can have immediate effects on the expression of traits in a population (Lande and Arnold 1983). These phenotypes are not fixed but can vary over the course of an individual's lifetime. Individuals can, therefore, acclimate to variation in environmental conditions (Stearns and Koella 1986, Kawecki and Stearns 1993, Ackermann and Doebeli 2004). The ability of a single genotype to produce multiple phenotypes across different environments is known as phenotypic plasticity, and can depend not only on abiotic environmental conditions but on biotic ones as well (Via and Lande 1985, Miner et al. 2005, Pigliucci 2005). Therefore, two individuals from the same species, or population, may develop different phenotypes if reared in even slightly different environments. This plasticity and diversification can allow individuals to exploit new niches when resources are limited or when competition is high. This means that selective forces vary among individuals of a given population (Schluter 2000, Bolnick et al. 2003). Phenotypic plasticity is thus widely accepted as being adaptive (Via and Lande 1985, DeWitt et al. 1998, Pigliucci 2005).

Given the ability of individuals to acclimate to a given environment, we should expect that phenotypes should perfectly match their environments. There are,

however, costs and limits to phenotypic plasticity. While the costs of phenotypic plasticity were initially lacked empirical data (DeWitt et al. 1998, Criscuolo et al. 2011) there are now hundreds of studies demonstrating the trade-offs in fitness that occur when adopting a particular phenotype with regard to a particular environment. It is now increasingly evident that not all individuals in a population, in a given environment, express the optimum phenotype. Furthermore, phenotypic plasticity can be constrained through species interactions (e.g. competition) (Callaway et al. 2003, Werner and Peacor 2003, Miner et al. 2005). The fitness of individuals, therefore, depends not only on their own phenotypes but on those of the entire community. Moreover, variation in the abiotic and biotic environment can interact with the variation in an individual's phenotype (Dingemanse et al. 2010, Stamps and Groothuis 2010, Wolf and Weissing 2010). That is, selective pressures can vary in space and time to generate phenotypic plasticity for traits that differ from one individual to another (Dingemanse and Réale 2013). Despite this, the variation of these traits in a population can serve as a potential buffer against fluctuations in the environment (Callaway et al. 2003).

Ecomorphology is one of many fields that study the proximate mechanisms by which individuals survive and reproduce successfully (Williams 1966, Karr and James 1975). It attempts to infer ecological relationships among species from their morphology. It also attempts to elucidate the functional relationship between morphology and ecology as it is mediated by the behaviour and performance of the organism (Wainwright and Reilly 1994). Most ecomorphological studies until now have compared how species and populations differ in their morphology and habitat use (Wiens and Rotenberry 1980, Schluter 2000, Adams 2010, Lailvaux and Husak 2014, Senay et al. 2015). Morphology and performance can, however, be plastic and subject to influence from both intrinsic and environmental factors. Plasticity in these traits can be adaptive in complex environments. Furthermore, complex environments

can impose many trade-offs that dictate resource allocation within an organism. Morphology, a fitness-related trait linked with performance can, in particular, experience strong context specific selection (Irschick et al. 2008) as even small changes in morphology can lead to large differences in performance (Koehl 1996).

Further complicating our understanding of the relationships of morphology and performance during an individual's lifetime are the definitions of morphology and performance themselves. Both morphology and performance can be considered as functional traits, which impact fitness indirectly via their effects on growth, reproduction, and survival (Arnold 1983, Pough 1989, Violle et al. 2007). Functional traits confer advantages to foraging, escaping predators, and finding a mate. These traits are thus often very good predictors of survival and reproductive success (Irschick 2003, Irschick et al. 2008) and are subject to diverse selective pressures (Lailvaux and Husak 2014). The term morphology can, however, actually refer to anything from size, colour, texture, and geometric shape (Adams et al. 2004, Zelditch et al. 2004, Adams and Otarola-Castillo 2013, Adams et al. 2013). Shape itself refers more specifically to the geometric shape of an individual or object once variation due to size colour, texture and any other variables has been removed. In this dissertation, I will be using the term shape and morphology interchangeably but it should be noted that whenever the term morphology is used, I am speaking of geometric shape. The definition of performance is much vaguer and could potentially be confused as an indirect measure of fitness itself. This generality has some conceptual advantages as it could be applied to any species or mechanical system from the force in Netwons in the contraction of some individual's quadriceps to the VO_2 max of a fish swimming at 23°C. Some authors have also used the term of whole-organism performance, which is defined as "any quantitative measure of how well an individual performs in a dynamic, ecologically relevant task measured at the level of the organism" (Lailvaux

and Husak 2014). Whole-organism performance traits require the allocation of resources to build rigid mechanical structures (Irschick et al. 2008, Lailvaux and Husak 2014). Trade-offs resulting from the allocation of resources to different systems can therefore directly impact whole-organism performance. For example, simple dietary restriction through competition or environmental variability will lead to a reduction in performance because the costly development of muscle and other morphological features is not possible (Lailvaux and Husak 2014). Exercise can also have a significant influence on morphology and whole-organism performance (Kieffer 2010, Palstra and Planas 2011). The definition of performance, though, still remains weak because many indirect measures of fitness have the same general definition. In that light, it is wise to clearly define what specific measurements of performance and of fitness are being used in a study. Despite these different definitions of morphology and fitness in the literature, many authors have attempted to incorporate these terms in general frameworks to guide their research in ecomorphology.

Arnold's (1983) conception of the ecomorphological paradigm was established to test the causal relationship between performance and fitness by including morphology, which he argued, was necessary to understand how variation in performance was generated. The model provided a framework to describe how variation in morphology determined performance and could lead to differences in fitness among individuals in a population (Figure 0.1 A). While influential, this model had its limitations. It was overly simplistic and has since been improved upon to incorporate other mechanisms by which morphology, performance and fitness could be influenced. One such expanded model was introduced by Garland and Losos (1994). They attempted to resolve some of the limitations and inflexibility of Arnold's model by taking habitat use, interspecific interactions, and behaviour into account (Figure 0.1 B). Others have

now gone so far as to incorporate many life-history traits into the ecomorphological model (Lailvaux and Husak 2014). These models too, however, can be overly simplistic as they fail to account for individual differences and phenotypic plasticity. Their scope is usually also limited to the performance of squamate lizards; though the authors of these models did decry the lack of experimentation in ecomorphology. This situation has not improved as a recent review has reiterated that still little is known about the factors that influence performance in most animals (Lailvaux and Husak 2014). More empirical evidence supporting the relationships outlined in the ecomorphological paradigm will help us understand how individuals and populations acclimate and adapt to complex environments.

A)

Morphology → Performance → Fitness

B)

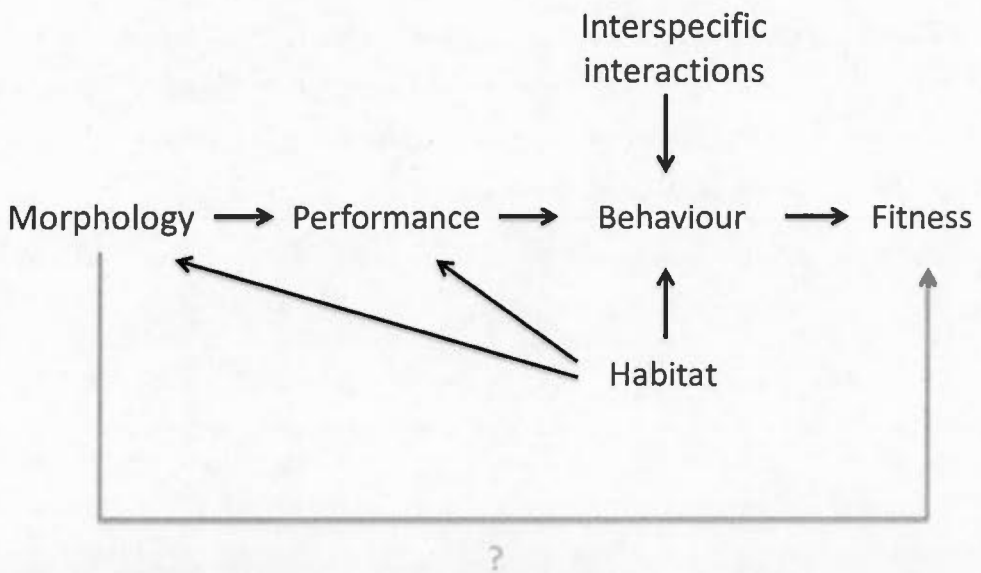

Figure 0.1 The ecomorphological paradigm. A) Arnold's original model (1983), and B) Garland and Losos' expanded model (1994).

This dissertation attempts to apply the concepts outlined in ecomorphology to an ecologically and economically important species, the Atlantic salmon (*Salmo salar*). I use Arnold's (1983) original framework as well as Garland and Losos' (1994) improvement of the framework as a starting point to test how variation in morphology and swimming performance influence growth in this species. I also expand these frameworks by testing for new relationships between these traits across

different complex environments in both field and laboratory studies. A special care is taken to account for individual differences among individuals and phenotypic plasticity as well as how these concepts could be applied to conservation management of this species at risk. The following sections will introduce the model species used throughout this dissertation and provide further background for several of the concepts that form this dissertation's backbone. Methods that are used throughout this thesis will also be described.

0.2 Conservation and the case of the Atlantic salmon

Humans have drastically altered ecosystems at all spatial scales and have put the goods and services which they provide at risk (Hooper et al. 2005). Freshwater ecosystems have been at particular risk (Beeton 2002, Brönmark and Hansson 2002, Dudgeon et al. 2005, Geist 2011). To mitigate the damages, conservation biologists and government agencies often target keystone species or habitats whose protection can indirectly benefit other species and the general health of the ecosystem (Paine 1969, Power et al. 1969, Bond and Lake 2003).

The loss of large predators in particular, whose presence in ecosystems often have cascading, top-down effects, can severely alter ecosystem functioning (Brönmark and Hansson 2002, Frank et al. 2005, Myers et al. 2007, Ellis et al. 2011). Some of the most commercially exploited fishes are, indeed, predators. Worldwide predatory fish biomass has diminished by at least 80% in the past few decades due to overfishing (Pitcher 2001, Myers and Worm 2003, Myers et al. 2007, Worm et al. 2009, Worm and Tittensor 2011). Targeting the top predators in an aquatic ecosystem for

conservation can restore and maintain ecosystem functioning (Baum and Worm 2009). Predatory fish such as some salmonids have been among the most exploited species of fish throughout human history (Worm et al. 2009). The role of fisheries management in maintaining and supplementing salmonid stocks or reintroducing populations to historic ranges has been that of breeding and rearing billions of fish for release (Kerr 2006, Gozlan et al. 2010, Neff et al. 2011). Despite these colossal efforts, there appears to be little success in restoring wild populations (Brown and Day 2002, Crawford and Muir 2007, Houde et al. 2015b). Re-establishing viable populations in the wild is notoriously difficult and the causes of failure are not well understood (Fischer and Lindenmayer 2000). The future of salmonid populations may depend on our understanding of their ecomorphology (Armstrong et al. 2003, Watters et al. 2003, Ciborowski et al. 2007, Garcia de Leaniz et al. 2007, Conrad et al. 2011)

Atlantic salmon were once an important native species in Lake Ontario and played a key ecological role as a top predator. However, they were extirpated from Lake Ontario by 1896 due to human activities and habitat loss (Huntsman 1944, Netboy 1968, Parrish et al. 1998). They are now officially considered extinct (COSEWIC 2010). Over the past three decades, conditions have improved in the Great Lakes, and since the early 1980's there has been a renewed effort to restore Atlantic salmon to Lake Ontario (Kerr and Ryder 1997, Beeton 2002, Diamond and Smitka 2005, Kerr 2006, Crawford and Muir 2007, Hasegawa 2016). Recent government-funded stocking programs have attempted to reintroduce Atlantic salmon using a number of source populations with ecologies and genetics similar to the historic population (Greig et al. 2003, Diamond and Smitka 2005, Kerr 2006). The restoration effort to date has focused on stocking at all life stages through artificial propagation in hatcheries (Stanfield and Jones 2003). Stocking efforts, however, have not yet produced significant results with only a few returning Atlantic salmon and limited

signs of sustainable natural production (Huntsman 1944, Greig et al. 2003, Stanfield and Jones 2003, Coghlan et al. 2007, COSEWIC 2010). Indeed, fewer than 5% of all hatchery-reared salmonids survive to adulthood (McNeil 1991).

Many factors are likely impeding the restoration of Atlantic salmon into Lake Ontario including poor survival, maladapted traits, lack of phenotypic diversity and both intraspecific and interspecific competition (Fausch 1988, Brown and Day 2002, Stanfield and Jones 2003, Neff et al. 2011, Houde et al. 2015b). For example, many of the tributaries in which Atlantic salmon used to flourish continue to be stocked with non-native salmonid species. The non-native salmonids, including Chinook salmon (*Oncorhynchus tshawytscha*), Coho salmon (*O. Kisutch*), rainbow trout (*O. mykiss*) and brown trout (*Salmo trutta*), were initially stocked to supplement the loss of Atlantic salmon and other large predators in the sports fishing industry (McKenna and Johnson 2005). These species, which now have self-sustaining populations in the Great Lakes, may be affecting the survival, growth, habitat use, behaviour and reproduction of Atlantic salmon (Scott et al. 2005a, Scott et al. 2005b, Scott et al. 2005c, Coghlan et al. 2007, Korsu et al. 2010, Hearn 1986). Newly stocked Atlantic salmon may be at a competitive disadvantage as they are no longer residents of the system (Hsu et al. 2005).

Juvenile Atlantic salmon are interesting as a model species, not only from a conservation context but also from an ecomorphological stance. They are among one of the most studied families of fishes and their ecology is well known (Aas et al. 2011). They also show a great diversity across a wide array of functional traits such as morphology, swimming performance, foraging strategies, and habitat use, which lends itself well to experimentation (Taylor 1991, Fraser et al. 2011). Furthermore, they are highly competitive, territorial, and undergo rapid growth once their

embryonic yolk sacs have been absorbed and they start actively feeding in the water column (Armstrong and Nislow 2006, Finstad et al. 2011, Nislow et al. 2011). Factors that influence performance in early life will have profound consequences on the fitness of the individual later in life.

0.3 Form and function

Most, if not all organisms are, to some extent, adapted to their environment and there are strong correlations between their morphologies, performance and general ecology (Losos 1990). The relationships between fish morphology, swimming mode and performance, and ecology is particularly well understood and there are common patterns in form and function in most species of fishes (Keast and Webb 1966, Blake 1983, Webb 1984, Arnold et al. 1991, Covell et al. 1991, Norton et al. 1995, Blake 2004, Peres-Neto and Magnan 2004, Senay et al. 2015). While the morphology of an individual has some genetic basis (Taylor and McPhail 1985), the environment, and in particular, stream velocity plays an important role in morphological differentiation among populations and individuals (Svåsand et al. 1998, Pakkasmaa and Piironen 2001, Solem et al. 2006, Kieffer 2010, Fu et al. 2013). Indeed, morphology directly influences the hydrodynamics of individuals and determines their ability to occupy different microhabitats within their landscape (Domenici and Blake 1997, Blake 2004).

Shape analysis itself has always been an important part of biological research and it has undergone a major revolution as multivariate statistical techniques have

improved. Linear measurements of morphological features often have low informational value as they lack the power to discriminate between specimens (Sokal and Rohlf 1995, Adams et al. 2004, Rohlf and Marcus 2005, Adams et al. 2013). Geometric morphometrics is a more robust tool to study shape variation and its covariation with other variables (Bookstein, 1991). As it plays a prominent role in this thesis, I will briefly describe how shape data is acquired and analysed. First, virtual landmarks are overlaid on digital photographs whereupon a Generalised Procrustes Analysis removes variation due to the orientation, position, and size of the specimens (Figure 0.2). The landmarks are then superimposed in a common shape space and their coordinates are obtained. From these coordinates or from partial warp scores calculated from the coordinates, we can compare the morphologies of individuals or populations using commonly used multivariate statistics (e.g. MANOVA, principal components analysis, discriminate function analyses) (Adams et al. 2004, Zelditch et al. 2004, Adams and Otarola-Castillo 2013, Adams et al. 2013). In this dissertation, I have used a number of software packages to place landmarks, run General Procrustes Analyses, acquire landmark coordinates and partial warp scores, and visualise the differences in morphology using thin-plate-splines to produce deformation grids. Each technique used is described in greater detail in the methods of each chapter.

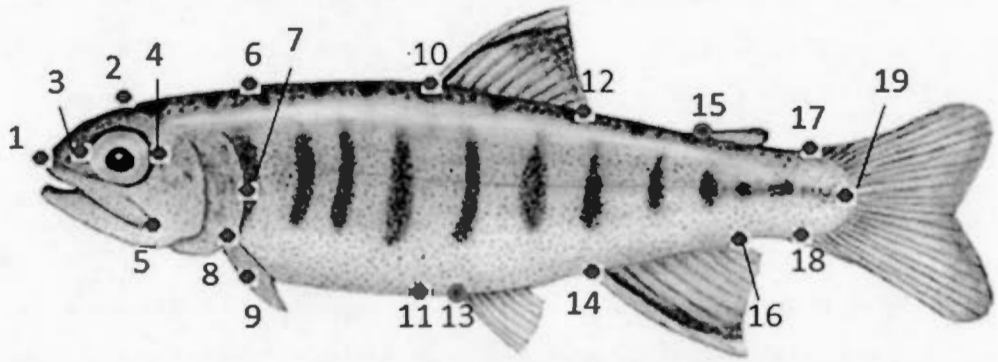

Figure 0.2 Juvenile Atlantic salmon with 19 homologous landmarks which were used for geomorphometric analyses: 1 anterior lip of the upper jaw; 2 head at the midpoint of the eye; 3 most anterior point of the eye; 4 most posterior point of the eye; 5 base of the maxilla; 6 dorsal point of head at the posterior edge of the operculum; 7 posterior edge of the operculum; 8 insertion of the pectoral fin; 9 ventral point of head at the posterior edge of the operculum; 10 anterior dorsal fin insertion; 11 ventral point opposite of the anterior dorsal fin insertion; 12 anterior insertion of pelvic fin; 13 anterior insertion of anal fin; 14 posterior insertion of dorsal fin; 15 posterior insertion of the anal fin; 16 anterior insertion of adipose fin; 17 dorsal terminus of caudal flexure; 18 ventral terminus of the caudal flexure; 19 most anterior point of caudal peduncle.

Swimming performance also plays a prominent part in this thesis and is a good predictor of fitness in fish as it is linked with their ability to acquire food and escape predation (Blake 2004). The swimming activity of many fish is commonly divided into two broad categories: prolonged, moderate speed, sustained swimming (used for station holding and general locomotion), and high speed, burst swimming (used to capture prey or avoid predation) (Blake 1983, Blake 2004). Prolonged swimming is commonly measured by calculating the critical swimming speed (U_{crit}) (Brett 1964). It is a purely aerobic form of locomotion and gives an estimate of the speeds an individual might be faced with in its environment and could sustain for a period of time between 2 and 200 minutes (Beamish 1978, Plaut 2001). Burst swimming, an

anaerobic form of locomotion, involves fast starts and rapid turns that last for a few seconds (Domenici and Blake 1997, Wakeling and Johnston 1998, Tierney 2011).

0.4 Personalities and variation in behaviour

The study of animal personality has taken off exponentially in the past few decades. From its origins in human psychology, it has it has now become a central concept in behavioural ecology (Carrere and Maestripieri 2013). Advances in this field have even come full circle, influencing the direction of research in human psychology (Gosling 2001, White et al. 2007, Wolf et al. 2007). While attempts have been made to standardise the terminology across the field, many definitions of personality, as well as the factors describing personality, still exist (Carrere and Maestripieri 2013). Care must, therefore, be taken in defining the terms for any study concerned with animal behaviour. For instance, in the past, personalities have been referred to as temperaments (Réale et al. 2007), behavioural syndromes (Sih et al. 2004), and coping styles (Koolhaas et al. 1999). Most now agree that differences in behaviour between individuals are relatively consistent over time and across contexts. Furthermore, many individual behaviours are frequently correlated with one another forming behavioural syndromes. For example, boldness is often correlated with aggressiveness and higher activity in individuals across a wide range of taxa (Réale et al. 2010). Dingemanse and Réale (2013) define personality as: "the [consistent] difference between individuals in their average level of [a given] behaviour". With this definition, correlated suites of behaviours are referred to as behavioural syndromes (Sih et al. 2004) and, it is these definitions that will be used throughout this thesis.

Inter and intra-individual variation in behaviour results from a complex interaction between phenotypic plasticity and environmental variability (McLaughlin et al 1994). Trade-offs can impede directional selection from fixing any one behavioural phenotype in a given population. There are now many mechanisms that we know of to explain how variation in behaviour is generated and maintained in populations (Dingemanse and Réale 2013). One compelling idea is that variation in the environment can interact with the variation in an individual's phenotype (Dingemanse et al. 2010, Stamps and Groothuis 2010, Wolf and Weissing 2010). That is, selective pressures can fluctuate in space and time and thus generate phenotypic plasticity and differences in behaviours among individuals in a population (Smith and Blumstein 2007, Dingemanse and Réale 2013). Behavioural syndromes may also constrain directional evolution since each behaviour might only be adaptive in certain situations and cannot be disentangled from other behaviours without incurring some fitness cost (Dochtermann and Dingemanse 2013). Trade-offs with other life-history traits also limit the directional selection of a given behaviour (Biro et al. 2006, Smith and Blumstein 2007, Wolf et al. 2007, Biro and Stamps 2008).

Behaviour was formerly assumed to be plastic over time and contexts in response to environmental variation (Bergmüller and Taborsky 2010). Animals, after all, have the capacity to learn, innovate, communicate with conspecifics and adopt different coping mechanisms to environmental and social stresses (Koolhaas et al. 1999, Danchin 2004, Dall et al. 2005). However, empirical evidence suggests that behaviours are not as plastic as previously assumed. They form these distinct aforementioned personalities that differ among individuals and are highly repeatable, heritable and prevalent across different taxa (Bell et al. 2009, Dingemanse et al. 2010, Van Oers and Sinn 2013). Since these differences in personality are consistent across different contexts, they raise many questions as to how they are maintained in

populations (Wolf et al. 2007). Indeed, if behaviours are correlated across time and in different contexts, then this behavioural spillover could be maladaptive in certain contexts. Individuals, therefore, may not always display the optimum behaviour for the environment. For example, aggressive individuals may have more success defending themselves against predation; however, the same behaviour in a different context, like reproduction, may result in fitness costs if the member of the opposite sex is driven away (Sih et al. 2004).

In this thesis, three commonly measured behaviours are considered: activity, boldness and aggressiveness. Activity is defined as the distance travelled in a safe and familiar environment while exploration is considered as the latency to explore a novel space (Réale et al. 2007, Montiglio et al. 2010, Conrad et al. 2011). Despite this distinction, it is difficult to disentangle them from one another and they are often highly correlated. Boldness is the willingness to expose oneself to risk (Ward et al. 2006, Réale et al. 2007). It can vary considerably over an individual's lifetime and across different life stages and is usually positively correlated with competitive ability (Bell and Stamps 2004, Biro and Stamps 2008). There is also evidence that boldness can be influenced by social group dynamics whereby the presence or absence of conspecifics facilitates the motivation to explore novel environments through the diffusion of risk (Ward et al. 2006, Magnhagen 2007, Borcherding and Magnehagen 2008, Keiser et al. 2014). In fishes and other species, boldness has often been measured in open field tests as the latency to approach a predator, enter a novel environment, or approach a mirror or conspecific (Martel and Dill 1993, Conrad et al. 2011, Balzarini et al. 2014, Toms and Echevarria 2014). Aggression among conspecifics is usually in the context of foraging for limited resources, be they food or reproduction opportunities (Lorenz 1963). Salmonids are among the few species to actively defend territories outside of a reproductive context through agonistic interactions with conspecifics (Keenleyside 1979, Nislow et al. 2011). The highest instances of aggression usually occur between

individuals with the largest differences in size and competitive ability (Fausch 1984, Puckett and Dill 1984, Fausch 1988). Aggression also varies as a function of group size and availability of resources (Sakakura and Tsukamoto 1998, Grant et al. 2002).

Activity, boldness, aggressiveness, and exploration are among the most studied of behavioural traits that form syndromes (Sih et al. 2004, Réale et al. 2007, Dingemanse et al. 2010). They are also correlated with a number of life history traits which may impact fitness (Smith and Blumstein 2007, Wolf et al. 2007, Biro and Stamps 2008, Réale et al. 2010). On one end of the spectrum, we frequently find individuals that are aggressive towards conspecifics, bold towards predators and show higher activity and exploration in novel environments. On the other side of the continuum, we find individuals that are consistently docile or submissive towards conspecifics, timid towards predators, and relatively sedentary. These relationships can, however, be modulated to a degree by environmental variation, both biotic and abiotic and this is thought to be adaptive (Bell and Sih 2007).

While classical behavioural ecology has long studied the effects of competition on foraging ecology, it is unclear how interspecific and intraspecific competition influence variation of behaviours both between and within individuals of a population across different environments. When is it advantageous to be plastic or consistent in a given behaviour? Do behaviours always form syndromes? Many of these questions are yet to be fully elucidated. For example, few studies have attempted to directly test how variation in behaviour, both among individuals and within an individual, can influence an organism's ecomorphology or its impact on fitness (Garland and Losos 1994).

0.5 Competition

0.5.1 Interspecific competition

All organisms interact with their neighbours and, although sufficient habitat heterogeneity may allow coexistence between species with similar niches, individuals may have to modify their phenotype to live in sympatry (Wiens 1989, Tilman 1994). Frequently, species living in sympatry that compete for similar resources evolved by shifting or reducing their niche breadth, reducing the costs of competition (Connell 1983, Schluter and McPhail 1992, Schluter 2000, Grether et al. 2009, Adams 2010). As such, these ecological character displacements are important drivers of selection (Robinson and Wilson 1994). Phenotypic plasticity may, however, be constrained among individuals in a population, as deviations away from locally adapted traits for a given environment, may result in decreased fitness (Sih et al. 1985, DeWitt et al. 1998, Fraser et al. 2011). Interspecific competition can usually be described by two broad mechanisms: exploitation (competitors indirectly reduce the availability of resources) and interference competition (individuals actively impede competitors from acquiring resources (Connell 1983, Wiens 1989). Fitness-related traits (e.g. growth) can be negatively impacted, as a consequence of the scarcity of resources and real or perceived physical danger. Although interspecific competition is prevalent in natural systems we do not know and have ignored how interspecific competition can affect fitness-related traits within an individual's lifetime (Grether et al. 2009).

Competition between fish in freshwater systems (i.e. lakes, rivers and streams) has been well studied (Simon and Townsend 2003). While competition has clearly shaped the benthic-pelagic paradigm in resource use and morphology in lake species there

has been some debate as to the importance of competition in stream fish in determining patterns of species distributions and community structure. As the environment in streams and rivers in more variable than that of lakes, it is assumed that variation in morphology, behaviour and other physiological adaptations among species would be more important than interspecific competition in determining community structure (Grossman et al. 1998). However, competition and other biotic factors have been shown to have comparable effects on fish communities in lakes and streams (Jackson et al. 2001, Senay et al. 2015). Indeed, different environments may promote different kinds of competition which can lead to differences between species (Garland and Losos 1994). It is theorised that this agonistic character displacement, caused by interference competition between one or more sympatric species, can result in evolutionary shifts in traits and have important consequences on other ecological processes (Grether et al. 2009).

Systems in which species were intentionally or accidently introduced present a different situation. Since the introduced competitive species would not have evolved alongside the native species, their initial responses to one another are not likely to be adaptive and competitive interference can occur (Grether et al. 2009). Competition for limited resources in these situations would presumably be strong and differences in competitive ability might result in a reduction of fitness in the native species (Gozlan et al. 2010). For example, asymmetric competitive ability can induce shifts in microhabitat use (Crow et al. 2010). If the preferred habitat of the native species is dominated by a new competitor, then the native species may be marginalised to poorer quality habitats which could have lasting effects on fitness-related traits (Sih et al. 1985).

Salmonids have been introduced intentionally and accidently well beyond their native range for economic reasons (Nislow et al. 2011) and there are many places worldwide where non-native salmonid species co-occur (Korsu et al. 2010). Pacific salmonids, as well as European brown trout, have been introduced into much of the original habitats of the North American Atlantic salmon (Crawford and Muir 2007, Finstad et al. 2011, Nislow et al. 2011). These invasive species of fish require similar resources and habitat types to survive, resulting in intense competition (Fausch 1988, 1998, Grant et al. 1998, Hearn 1986). Brown and rainbow trout are among the IUCN top 100 worst invasive species list (Lowe et al. 2000). Nonetheless, few studies have experimentally tested the direct effects of the non-native species on the fitness of Atlantic salmon (Beall et al. 1989, Stanfield and Jones 2003, Korsu et al. 2010, Houde et al. 2015c). Atlantic salmon are normally found in relatively simple community assemblages that are species poor and dominated by interference competition. Exploitative or interference competition from introduced species may, however, have dire consequences on Atlantic salmon fitness (Fausch 1988, 1998, Nislow et al. 2011). It is unclear what the magnitude of interspecific competition would be on Atlantic salmon survival and how it would interact with individual variation in behaviour and morphology across different habitats to influence performance and fitness.

0.5.2 Intraspecific competition

Interspecific competition and predation are often considered some of the greatest selective forces on the behaviour and morphology of individuals (Sih et al. 1985, Lima and Dill 1990); however, intraspecific competition may exert an even stronger selective pressure (Lorenz 1963, Sih et al. 1985, Robinson and Wilson 1994, Ward et

al. 2006). Intraspecific competition is a diversifying force that creates differences within species or populations in the absence of interspecific competitors (Robinson and Wilson 1994). If individuals change their realised niche, they could reduce the costs of competition. It follows that individuals must be able to recognise members of their own species or population.

Fish are able to discriminate among conspecifics in a variety of ways, from visual to chemosensory recognition (Ward et al. 2007, Ward 2014). This ability to recognise conspecifics helps shape their social structure to the point that some social species of fish are able to recognise weaker competitors and preferentially shoal with them (Ward et al. 2007). Salmonids are no exception to this rule and rely on both visual and chemical cues in identifying conspecifics and kin, as well as risky habitats, during their lives (Stabell 1987, Moore et al. 1994, Courtenay et al. 1997, Kim et al. 2011). Chemical alarm cues, in particular, can lead to morphological and behavioural adaptations, even in the absence of visual stimuli, alerting individuals to distressed conspecifics and dangerous situations (Brown 2003). It is well established that stimuli emanating from species that prey upon the focal species can induce phenotypic change (Martel and Dill 1993, Martel 1996, Bell and Sih 2007, Chivers et al. 2007, Kim et al. 2011); though, much less is known about how intraspecific competition can influence plasticity (Blanchet et al. 2008, Kim et al. 2011).

Intraspecific competition for resources in fish is shaped by the distribution of resources in space and time and is often size and age dependent. Larger individuals are generally more efficient foragers than smaller individuals of the same species. They are faster swimmers, have a higher visual acuity and are more physically imposing than their smaller counterparts (Milinski and Parker 1991a, Ward et al.

2006). However, the competitive ability of an individual will depend not only on its physical traits (e.g. size) but on its behaviour and the foraging strategies used to acquire and defend resources in a given environment. In fact, boldness and aggression are both correlated with competitive ability in juvenile Atlantic salmon and may be more important to their competitive ability than size (Huntingford et al. 1990b). Aggression is an integral part of a salmon's foraging strategy and their competitive ability will have a direct link on their fitness. The amount of aggression shown will depend on a number of factors, including time spent foraging and the energy acquired from different patches (Lorenz 1963, Puckett and Dill 1984). Foraging behaviour will thus be the result of a trade-off between acquiring energy, expending it through acquiring said resources and, defending those resources through agonistic interactions with conspecifics. Grant (1997) suggested that a number of factors could influence this trade-off (e.g. competitor density, resource abundance, spatial and temporal clumping of resources and spatial and temporal predictability of resources). For example, in habitats with limited resources and high densities of competitors, subordinate individuals may switch to lower quality resources rather than incur injury (Milinski 1982).

Salmonids are territorial foragers and require an abundant source of invertebrate drift for growth (Keenleyside 1979). An individual's territory is the result of a trade-off between foraging opportunities and the energetic costs of holding station in faster-moving currents, which have a higher abundance of invertebrate drift (Keeley and Slaney 1996). Territory size is often inversely related to food abundance and to population density. More productive streams would, therefore, have a greater density of fish with smaller territories (Keeley and McPhail 1998, Keeley 2000, Imre et al. 2004). Similarly, the size of the territory defended is greater in larger individuals in order to meet their energetic demands (Keeley and Slaney 1996). Thus, larger and/or more dominant Atlantic salmon may spend more time defending a territory than

acquiring resources and may be less likely to feed in new environments (Sakakura and Tsukamoto 1998, MacLean et al. 2000, Cutts et al. 2002). Aggressive behaviour and foraging strategy are, thus, context specific and switching to a different strategy could be beneficial for acquiring resources (Stearns and Koella 1986, Dingemanse and Réale 2005, Conrad et al. 2011). Indeed, intraspecific competition should increase the breadth of a species' niche (Connell 1983). However, recent studies in animal personality show that individuals may show consistent behaviour across a variety of environments (Sih et al. 2004, Bell et al. 2009, Dingemanse et al. 2010) which could affect their relative competitive ability relative to conspecifics. Together with interspecific competition, the effect of intraspecific competition on phenotypic plasticity within individuals across different habitats remains unclear and warrants study.

0.6 Habitat

Environmental variability in freshwater ecosystems is important in structuring fish communities and contributes to the diversification of traits both between and within populations (Ackermann and Doebeli 2004, Peres-Neto 2004, Ward 2006, Roberts et al. 2011). A meta-analysis of 92 fish species found that habitat heterogeneity, along with competition and predation, had strong effects on the diversification of phenotypic traits (Robinson and Wilson 1994). For both lake and stream fishes, habitat segregation appears to be the most prevalent mechanism for promoting the evolution of resource partitioning (Grossman and Freeman 1987, Grossman et al. 1998). If fish species have similar habitat needs, then homogenous environments can result in intense competition. Heterogeneous environments, on the other hand, can

favour rapid adaptive radiation in systems where competition is present (Rainey and Travisano 1998).

Habitat complexity plays a critical role in the development of the morphology, behaviour and other physiological traits of fish (Kawecki and Stearns 1993, Roberts et al. 2011). For example, hatchery-reared fish are raised in relatively featureless holding tanks with extremely low habitat complexity. It is now widely accepted that fish raised in simple hatchery environments are maladapted to the wild when released and experience higher rates of mortality (Henderson and Letcher 2003, Roberts et al. 2011, Thorstad et al. 2011). Fish raised in hatcheries forage less efficiently (Solem et al. 2006, Larsson et al. 2011), take longer to detect and avoid predators (Álvarez and Nicieza 2003), are less successful at locating and claiming quality territories (Metcalfe et al. 2003), display inappropriate reproductive behaviours (Fleming et al. 1996), have less ability to react to environmental stimuli (Koolhaas et al. 1999), are poorer swimmers (McDonald et al. 1997) and, are more prone to predation as they are bolder towards new objects and predators (Sundstrom 2004, Höjesjö et al. 2011). In addition, salmonids raised in the artificial, simple habitats found in hatcheries show more aggression than wild fish but a reduced ability to compete for quality territory (Fleming et al. 1996, Metcalfe et al. 2003, Weber and Fausch 2003). Experimental studies have shown that environmental enrichment may reduce maladaptive behaviour in hatchery-reared salmon (Roberts et al. 2011). Specifically, hatchery fish were less willing to leave a refuge during a simulated predator attack when they were raised in habitats with live prey and refuges in the form of woody debris.

Providing heterogeneous habitats as well as promoting adaptive traits in individuals is essential to the successful restoration of freshwater ecosystems (Bond and Lake

2003). Juvenile salmonids occupy fast flowing, freshwater riffles and pools of streams with rocky substrate and plenty of woody debris, both of which can provide refuges (Finstad et al. 2011) and, they will position themselves in sections of the streams which allow them to efficiently manage their energy expenditure (Rosenbauer 1988). While the specific habitat requirements for wild Atlantic salmon are well documented (deGraaf and Bain 1986), due to the particularities of their life history, these habitat requirements vary both in space and time as the salmon mature. There is, therefore, an extensive diversity of habitats used by Atlantic salmon both between individuals and populations (Finstad et al. 2011). In general, the habitat requirements of juvenile Atlantic salmon change in function of their size. Fry occupy shallow, slow flowing sections of streams with gravel beds, while parr prefer to occupy sections of streams that are both deeper, faster and with larger sizes of rocky substrate which provide refuge from predation and agonistic interactions with competitors (Keeley and Grant 1995, Keeley and Slaney 1996, Stanfield and Jones 2003). Indeed rocky substrate cover is one of the best predictors of Atlantic salmon density in the wild (Stanfield and Jones 2003, Enders et al. 2007a, Enders et al. 2007b). However, while Atlantic salmon are generally central place foragers, the availability of resources found within their stream environments is highly variable in space and time. As a result, their territories are more fluidly dynamic than previously thought and individuals have been shown to be highly mobile at times, opportunistically investigating other microhabitats, leading to fierce competition among individuals (Armstrong et al. 1999, Nislow et al. 1999, Steingrímsson and Grant 2003, Roy et al. 2013).

0.7 Dissertation outline

The goal of this dissertation was to expand upon the ecomorphological paradigm and explore how the interactions between individual variation in morphology, performance and behaviour could influence fitness-related traits across different environments. As has been previously stated, the ecomorphological paradigm has rarely been tested outside of studies on adaptive radiation, primarily in lizards, despite multiple calls for more empirical studies. Furthermore, many potential relationships between the different factors of the framework have been ignored despite some fairly intuitive and implicit relationships. To that end this dissertation has not only tested how variation in morphology and swimming performance relate to growth in juvenile Atlantic salmon but also explores new relationships among these factors and how they are modulated by genetics, competition, and individual and group behaviour across different environments. This dissertation is comprised of four related chapters that explore different facets of these relationships.

Chapter 1	The effects of morphology on performance and habitat choice in two populations of juvenile Atlantic salmon
Chapter 2	Effects of competition on fitness-related traits
Chapter 3	Environmental variation influences intraspecific competition, individual morphology and growth in a hatchery-reared fish
Chapter 4	Behavioural and morphological plasticity interact across different environments to influence growth

In Chapter 1, I evaluated to what extent variation in morphology could influence swimming performance. To do this I first tested whether LaHave and Sebago Atlantic salmon, as well as their reciprocal hybrids, differed in their morphological variation

and how this related to their swimming performance. I used mixed models to partition the variance due to genetics and examine its contribution to individual morphology, mass and swimming performance. I hypothesised that each of these traits would have a fair degree of additive genetic variance and that there would be a strong relationship between morphology and swimming performance regardless of strain. I also tested whether there was a relationship between individual morphology and habitat choice in the wild. I hypothesised that individuals would disperse and sort themselves according to their morphology as it relates directly to swimming performance. In Chapter 2, I explored how interspecific competition could impact individual growth, morphology, and swimming performance. To do this I tested how LaHave and Sebago responded, in controlled experiments, to interactions with four other species of salmonids which are common competitors to Atlantic salmon in the Great Lakes of North America. I hypothesised that interspecific competition would reduce swimming performance and would lead to the development off maladapted morphologies in Atlantic salmon. In Chapter 3, I tested how the spatial distribution of resources and group density could interact to influence growth and morphological variation. To do this I experimentally manipulated fish density and resource distribution for both LaHave and Sebago in artificial streams over a week. I hypothesised that competition would be stronger when resources were clumped and fish density was high and that larger individuals would have a competitive advantage over smaller individuals. The different treatments would, therefore, lead to asymmetric competition and different growth and morphological development. Finally, in Chapter 4, I expanded upon my findings in Chapter 3 and investigated how individual behaviours were linked to growth and morphology in a heterogeneous environment. Once again I manipulated the spatial distribution of resources and fish density for both strains but I also measured individual behaviour before and after these manipulations. I hypothesised that individuals would be consistently different in their behaviour among each other across different contexts but that their growth and morphology would differ across treatments. Together, these four chapters led to significant findings that expanded

upon the ecomorphological paradigm and showed how these findings could lend insight into the management of Atlantic salmon in a conservation context.

CHAPTER I

THE EFFECTS OF MORPHOLOGY ON PERFORMANCE AND HABITAT CHOICE IN TWO POPULATIONS OF JUVENILE ATLANTIC SALMON

1.1 Abstract

Hatchery-reared fish often have lower fitness than their wild counterparts when introduced into a natural environment. This presents a serious problem for fisheries managers as they attempt to establish viable populations. Understanding which phenotypes are linked with performance may be a way to improve the success of these programs. Variation in morphology among individuals in a population is known to determine variation in performance which in turn will impact fitness. This study quantified the variation in morphology (shape components) of two hatchery-reared strains of juvenile Atlantic salmon and evaluated how this variation related to individual swimming performance. We tested fish produced from a 2x2 factorial mating design to evaluate both pure half-sibling families from each strain, as well as their reciprocal hybrids. Second, we evaluated how morphology influences habitat choice. We did this by releasing several thousand juvenile Atlantic salmon from each strain into streams and allowing them to disperse according to their phenotypes. We recaptured individuals and linked their morphologies to various microhabitat characteristics. We found that variation in morphology significantly influenced swimming performance but that genetic effects were less important. We also observed no differences in swimming performance between pure and hybrid families. Finally, we found a significant relationship between microhabitat choice and

morphology. We were able to distinguish between individuals released in different streams and match them to particular sections of the streams which were characterised by specific microhabitats based solely on their morphologies. The results suggest that considering morphological variation is critical for fish translocations as they can influence swimming performance and habitat choice

1.2 Introduction

Controlled releases of hatchery-reared salmonids have been a central tenant in those species' conservation management strategies (Huntsman 1944, Greig et al. 2003, Stanfield and Jones 2003, Diamond and Smitka 2005, Coghlan et al. 2007). However, re-establishing self-sustaining populations is difficult as domesticated salmonids have low survival in the wild (Johnsen and Ugedal 1989, McNeil 1991, Fischer and Lindenmayer 2000, Fraser 2008, Thorstad et al. 2011, Houde et al. 2015b). Hatcheries regularly breed for traits that are desirable for mass production such as increased growth rate, early reproductive performance and early maturation (Gall and Huang 1988a, b). While larger body size is usually a good predictor of fitness in fish (Metcalfe et al. 1989, Ward et al. 2006, Dmitriew 2011), faster growth rates in early life result in trade-offs that lead to decreased longevity and performance (Mangel and Stamps 2001, Metcalfe and Monaghan 2003, Álvarez and Metcalfe 2005, Álvarez and Metcalfe 2007). Furthermore, the homogeneous environment of hatcheries can result in low phenotypic variation leading to individuals with traits maladapted to their environment once released (Brown and Day 2002, Watters et al. 2003, Kawecki and Ebert 2004, Neff et al. 2011, Roberts et al. 2011).

Variation in fitness-related traits should allow individuals to occupy and acclimate to a greater variety of niches once released in the wild (Schluter 2000, Watters et al. 2003, Houde et al. 2015b). Morphology and swimming performance vary considerably among species and populations of fishes and are linked to many aspects of an individual's ecology such as habitat use, foraging behaviour, predator evasion, and territorial defence among others (Garland and Losos 1994, Norton et al. 1995, Lailvaux and Husak 2014). While habitat based patterns in fish morphology and swimming performance have been well studied across species and populations (Peres-Neto and Magnan 2004, Solem et al. 2006, Peake 2008, Solem and Berg 2011, Senay et al. 2015), less attention has been accorded to intra-population variation in these traits and their potential impact on conservation initiatives. Streams are complex environments with a diversity of microhabitat characteristics which imposes many different selective pressures among individuals in a population (Heggenes and Saltveit 1990, Wood and Bain 1995, Grossman et al. 1998, Magoulick 2000, Irschick et al. 2008, Harrison et al. 2015). While salmonids have a large degree of adaptive variation in morphology (Taylor 1991, Garcia de Leaniz et al. 2007, Fraser et al. 2011), hatchery-reared salmonids typically develop different morphologies and have less morphological variation than their wild counterparts (Rouleau et al. 2010). Furthermore, they tend to be weaker swimmers (Solem et al. 2006, Rouleau et al. 2010, Pulcini et al. 2013). Understanding the variation in these traits could, therefore, contribute to successful translocations of hatchery-reared salmonids.

Full factorial mating designs, in which males and females are crossed in all possible combinations, are used increasingly to produce not only genetic diversity but to study genetic quality and phenotypic variation (Lynch and Walsh 1988, Pitcher and Neff 2006, Neff et al. 2011, Houde et al. 2013, Houde et al. 2015a, Houde et al. 2015b). Examining the genetic architecture of a population can allow fisheries programs to

target the genes that underlie fitness and fitness-related traits in their breeding programs (Neff et al. 2011). Good genes are characterised by additive genetic variance and are linked with fitness and directional selection in populations regardless of the rest of the genome. Compatible genes show non-additive genetic variance and indicate favourable gene-gene interactions between sire and dam. Maternal variance is composed of the maternal genetic and maternal environmental effects and is known to have a large influence on early life survival (Neff and Pitcher 2005, Pitcher and Neff 2006). Additive genetic variance has been used extensively to study the adaptive potential of salmonid populations for many life-history traits linked with fitness (Carlson and Seamons 2008). The importance of non-additive genetic effects on fitness has also been established in juvenile Chinook salmon (Pitcher and Neff 2006, Evans and Neff 2009), Atlantic salmon (Houde et al. 2013, Houde et al. 2015a), and rainbow trout (Rye et al. 1990). Maternal (environmental) effects are important for early survival and are associated with many fitness related traits in juvenile salmonids, though due to ontogenetic shifts, their importance generally decreases over time (Robison and Lumpert 1984, Beacham 1989, Heath et al. 1999, Houde et al. 2013, Houde et al. 2015a). There is nonetheless some evidence to suggest that the maternal environment can impact performance later in life (Jonsson and Jonsson 2014). Despite these advances, there are few studies that have evaluated the genetic architecture of juvenile swimming performance, and relevant fitness-related traits (Green and McCormick 2005, Huuskonen et al. 2009, Nadeau et al. 2009, Kekalainen et al. 2010, Humphrey 2011).

Salmonids are well known for their phenotypic plasticity and rapid local adaptation to environmental variation (Taylor and McPhail 1985, Taylor 1991, Hendry 2000, Hutchings 2007, Fraser et al. 2011). However, translocated populations may not comprise sufficient morphological variation to occupy their new habitat. For

example, if the velocity of the stream into which hatchery-reared salmonids are released is too rapid, and the population lacks the morphological variation and associated swimming performance necessary to occupy that environment, then few if any individuals will survive there. There is increasing evidence that individuals do not just move randomly in a landscape but adjust their habitat choice decisions based on their phenotype. This phenomenon is known as phenotype-dependent habitat choice, or habitat matching (Bolnick et al. 2003, Edelaar et al. 2008, Bolnick et al. 2011, Dall et al. 2012, Jacob et al. 2015). Finally, microhabitat variation in streams is extremely diverse, with variation in important environmental characteristics changing dramatically within a few meters (Peres-Neto 2004; Senay et al. 2015). Habitat matching can be a useful tool for conservation or reintroduction efforts. Instead of stocking individuals based on age or size (Gall and Huang 1988a, b), we can potentially match individuals phenotypically to a given environment based on relevant traits such as morphology and swimming performance. Over time, phenotypic plasticity and selection may result in local adaptation to environmental conditions but the initial occupation of a niche still requires an appropriate phenotype (Taylor 1991, Edelaar et al. 2008).

Years of supplemental stocking have yet to produce a viable self-sustaining population of Atlantic salmon in Lake Ontario. Two strains (LaHave and Sebago), each with similar genetic and ecological backgrounds to the original Lake Ontario population, have recently been studied as potential source populations for large scale reintroductions (Huntsman 1944, Netboy 1968, Parrish et al. 1998, Diamond and Smitka 2005). While there is a risk of outbreeding depression and reduced performance when more than one source population is used for reintroduction, there is some evidence that controlled full-factorial mating between different source

populations can be used to target specific fitness-related traits such as growth (Wang et al. 2006, Houde et al. 2015b).

In this study, we evaluated how individual morphology and the genetic architecture of the two strains of juvenile Atlantic salmon could contribute to swimming performance. We hypothesised that each strain and their reciprocal hybrids would differ in morphology and swimming performance despite being raised in a common garden and that these differences would be due to genetic variation. We also hypothesised that swimming performance would be strongly associated with a streamlined morphology. We also tested whether the morphology of either strain could influence their habitat choice when released in the wild. We hypothesised that there would be a strong relationship between individual morphology and the microhabitat characteristics of where individuals were sampled. Understanding how variation in fish morphology impacts swimming performance and how morphology is linked with various microhabitat characteristics could contribute to the success of reintroduction programs.

1.3 Materials and methods

This study was composed of two parts. First, we estimated how genetic and morphological variation contributed to swimming performance in LaHave and Sebago juvenile Atlantic salmon as well as their reciprocal hybrids. Second, we tested whether individuals would choose habitats based on their morphologies. To do this, we released several thousand parr from each strain into three tributary streams that feed into Lake Ontario. After several weeks, we returned to recapture surviving

individuals and contrasted their morphologies and their differences in microhabitat variables, which characterised the stream sections from whence they were caught.

1.3.1 Subjects

Atlantic salmon from two populations were used in this study: "LaHave" from LaHave River (NS, Canada; 44.4°N, 64.5°W), and "Sebago" from Sebago Lake (ME, USA; 43.9°N, 70.6°W). LaHaves have been maintained by the Ontario Ministry of Natural Resources and Forestry (OMNRF) hatcheries for five generations and Sebagos for two generations.

For the first part of this study, reproductive adults from both the Sebago and LaHave strains maintained at the OMNRF Codrington Fisheries Research Facility (44.18.05°N, 78.29.40°W), were randomly selected to create 20 distinct half-sibling family blocks. These 20 family blocks were created using a 2x2 breeding design (i.e. a blocked full-factorial North Carolina Design II) (Lynch and Walsh 1988), using one female and male from each strain to produce half-sibling family blocks consisting of a pure Sebago cross (S/S), a pure LaHave cross (L/L) and their reciprocal hybrids (LaHave dam/ Sebago sire (L/S) and Sebago dam/ LaHave sire (S/L)). Each adult was used in only one 2x2 cross, resulting in 20 independent family blocks. The full factorial breeding design allows for the separate evaluation of intrinsic genetic factors including additive, non-additive and maternal effects (Pitcher (Lynch and Walsh 1988, Neff and Pitcher 2005, Neff et al. 2011). The eggs for the blocks were fertilised in the autumn of 2012. After fertilisation, the eggs from each separate cross were

randomly allocated to the cells of two separate incubation stacks, to control for block effects, each containing five trays with 16 cells per tray.

Eggs were placed in subdivided Heath incubation trays until they hatched (~3 months post-fertilization). The ambient water temperature during incubation mimicked natural conditions because water supplied to the incubation trays was from a spring-fed stream. Survival of the fertilised eggs was monitored three times a week until the latest date of hatching. Dead eggs were determined by visual inspection and removed from the trays as they occurred. At 5 months post-fertilization, individuals transitioned from endogenous feeding (yolk sac) to exogenous feeding. Individuals were then fed *ad libitum* using organic fish pellets (EWOS Commercial Feeds, Bergen, Norway).

Once alevins had absorbed their yolk sacs and manual feeding began, around 100 individuals (97 ± 2) from each full sibling cross were transported from the incubation trays and randomly allocated into separate 40 L family rearing tanks at the University of Windsor Great Lakes Fish and Research Centre in LaSalle, Ontario. Water quality (dissolved oxygen, pH, and temperature) was examined daily to ensure families were being held at optimal water conditions. On April 29, 2013, each tank was manually thinned down to 50 individuals to accommodate growth and limit density effects on the early growth of the fish in this critical period. Between May and June 2013, 3 randomly selected family blocks out of the 20 were chosen to test for variation in individual morphology as well their critical swimming speeds (Brett 1964). We measured 20 individuals per half-sib family (S/S, L/L, S/L, and L/S) for each of the 3 family blocks for a total of 240 individuals.

For the second part of this study, fish from each strain were produced by crossing gametes from 5 males and 5 females in all pairwise combinations (n = 25 families per population) to produce two 5x5 full factorial breeding designs (Lynch and Walsh 1988) from the same pool of reproductive adults kept at the OMNRF Codrington Fisheries Research Facility used in the morphology-performance study (see above). Fish released in Duffins Creek were produced in November 2010 and fish released in Cobourg Creek were produced in November of 2012. The LaHave and Sebago strains were crossed at the OMNRF Harwood Fish Culture Station (Harwood, ON) and transferred to the OMNRF Codrington Research Facility within 6 hours of fertilisation. Early life rearing protocols were identical to the first part of the experiment (see above).

Once alevins had absorbed their yolk sacs and manual feeding began, the Atlantic salmon fry were pooled by strain into large round tanks (~ 2000 per tank) and were held there until preparations were made for their release into the natural streams, in the spring of 2011 and the fall of 2013 respectively. For their release, the fish were transported in aerated Boanar tanks (4x4ft) to the three field sites from the Codrington Fisheries Research Facility. To prevent temperature shock, fish were slowly acclimated to the natural streams' respective temperatures, in large plastic bags filled with oxygenated water used for transportation, following OMNRF current stocking release protocols. They were transferred to the stream directly by hand-netting a few fish at a time, and gently placing the fish into the stream. The fish were placed into the streams over a 100-200 m stretch of stream to encourage spreading out into natural densities.

1.3.2 Study sites

Three streams were used in the release-recapture component of this study to observe how morphology variation matched across different habitat characteristics. All streams are stretches of tributaries which feed into Lake Ontario on the Canadian side of the border. The first two sites were located within East Duffins Creek, North of Ajax Ontario, (henceforth Duffins 1 and Duffins 2). Duffins 1 was located at 8th Concession Bridge (43° 57' 54" N 79° 4' 51" W). Duffins 2 was located at Whitevale Bridge (43° 54' 32" N 79° 4' 6" W). The third site was located in a stretch of Cobourg Creek located between Jibb and Bickle Hill roads in Cambome Ontario (44°02'04" N, 078°13'15" W). As in many studies in which Atlantic salmon were released into streams, the three sites were chosen to be relatively similar in temperature, productivity microhabitat variables and well suited for stocking juvenile Atlantic salmon (Heggenes and Saltveit 1990, Heggenes et al. 1999, Nislow et al. 1999, Finstad et al. 2011). All three sites have been used previously by the OMNRF for Atlantic salmon juvenile stocking. Duffins 1 and 2 were stocked in May of 2011 and sampled 5 months later in October of 2011. A total of 1890 parr (1444 LaHave/ 1446 Sebago) were stocked in Duffins 1 and a total of 1926 parr (1469 LaHave/ 1457 Sebago) were stocked in Duffins 2. Differences in numbers stocked between the populations were due to mortalities of juveniles while being reared at the OMNRF Codrington Fisheries Research Facility. The Cobourg site was stocked with a total of 2200 parr (1100 LaHave/ 1100 Sebago) in November of 2013 and sampled 1 month later in December of 2013 before the first snowfall of the season.

1.3.3 Swimming performance

Critical swimming speed (U_{crit}) was measured in an acrylic swim flume (Loligo Systems, Denmark). Subjects were placed individually into the swim chamber and left to acclimate for 10 minutes at a base velocity of 0.25 m/s. Flow speed was then increased by approximately 0.22 m/s every 2 minutes until they showed signs of fatigue. Fatigue was determined as when a fish could no longer actively swim against the current and was swept back against the mesh at the back of the chamber even after a mild voltage (5-10V) electric pulse was used to elicit movement. Critical swimming speed (U_{crit}) was calculated as ($U_{crit}=U_i + (T_i/T_{ii} \text{ X } U_{ii})$ for each individual (Brett 1964, Plaut 2001), where *Ui* is the highest velocity maintained for a full 2 minute interval, *Ti* is the time of fatigue at last current velocity (minute), *Tii* is the interval length (2 minutes), and *Uii* is the velocity increment (0.22 $m \cdot s^{-1}$). While many variations of this protocol exist, they are typically designed for adult fish and so shorter time intervals (2 minutes) were used to simulate the stream environment of juvenile Atlantic salmon where there are daily and seasonal fluctuations in water velocity (Peake 2008, Tierney 2011).

1.3.4 Microhabitat measures and electrofishing

Microhabitat characteristics, for all three streams, were measured the day after recapture. Microhabitat measurements were collected at 10 m intervals throughout the study sites (see Peres-Neto 2004 for additional details). Microhabitat measures taken were: (i) average cross-sectional stream water depth was calculated every 50 cm along the entire cross section; (ii) cross-sectional stream width from bank to bank along the entire cross section; (iii) average cross-sectional stream water velocity from measurements at 2–3 points along the cross section using a 10 second average measurement for each point using a digital flowmeter (Höntszsch, Germany); (iv) stream substrate coarseness estimated visually from the centre of the cross section in

the area bounded 1 m upstream and 1 m downstream along the cross section by percentage composition of clay (<0.002 mm), silt (0.002–0.05 mm), sand (0.05– 2 mm), gravel (2–60 mm), pebbles (60–150 mm), and cobble (>150 mm). Visual classification of substrate coarseness was based on a modified Wentworth scale (Heggenes and Saltveit 1990) and was recorded by the same individual for all sites to ensure the consistency of measurements.

Atlantic salmon juveniles from all three sites were captured using a backpack electrofisher (Halltech Aquatic Research, Guelph, ON, Canada) and a lip-seine net. Electrofishing started 500 m downstream of the initial release sites and moved upstream until about 100 m upstream of the initial release sites following a single pass zigzag pattern to ensure the greatest sampling coverage. The entire stream area was sampled. There was greater coverage sampling downstream than upstream because the majority of fry disperse downstream, usually within 500 m of the release point, within the first year (Einum et al. 2011). Captured individuals were held in large 10 L buckets filled with stream water until a predetermined stream section was completed. Stream sections were defined as areas roughly 30 m in length that contained homogenous habitat. These stream section boundaries were matched to the microhabitat survey described above, with each section containing a relatively equal number of microhabitat measures therein depending on the morphology of the stream. Duffins 1 and 2 both contained 13 sections and Cobourg Creek contained 9 sections. Subjects from each section were lightly anaesthetized using food-safe clove oil (Hilltech Canada, Vankleek Hill, ON, Canada, 100 ppm) and weighed using a digital scale. A digital photograph of each individual's left side was taken, against a white backdrop with a scale for reference, was taken for later geometric morphometric analysis. A small fin clip (<0.15 cm^2) was also collected from one of the caudal fin lobes and stored in 95% ethanol and placed in an icebox for later genetic assignment

to strain. Following these measures, subjects recovered in fresh stream water supplemented with a portable aquarium oxygen bubbler and were subsequently returned to the section from where they were originally captured. Non-target species from each section were identified to species, counted, and immediately returned to the water, downstream of electrofishing.

1.3.5 Morphology

For both parts of this study, nineteen fixed homologous landmarks (Figure 1) were placed on digital photographs of each individual using the tpsDig2 software (Rohlf and Marcus 2005). The homologous landmark coordinates were then analyzed using Generalised Procrustes Analysis (Zelditch et al. 2004). The resulting Procrustes-aligned coordinates were then analysed using multivariate statistics (see Statistical Analyses below).

1.3.6 Statistical analyses

To test whether and how the genetic architecture of the dam and/or sire influenced swimming performance, we estimated the additive genetic, non-additive genetic and maternal effects variance components (Lynch and Walsh 1988, Neff and Pitcher 2005) based a generalized linear mixed-effect model using the 'observLmer' functions in the 'fullfact' package in R (Houde and Pitcher 2016). We modelled U_{crit} using dam, sire and dam by sire as random effects. Family block was included as an

additional random effect, and cross type and body mass as additional fixed effects. We compared this full model to reduced models using AIC (i.e. mass excluded, cross excluded, and both mass and cross excluded). From here, we proceeded in testing how variation in morphology influenced swimming performance using generalized linear mixed models (GLMM).

Principle components analysis (PCA) was used on the Procrustes-aligned coordinates using R's base princomp() function to obtain multivariate morphological scores describing most of the variation in the Procrustes-aligned coordinates. These were subsequently used in GLMMs to determine how the morphologies of pure and hybrid half-sib families of LaHave and Sebago strains were related to swimming performance. The full model consisted of U_{crit} as a response variable, the principal component scores of the Procrustes-aligned coordinates, and cross (L/L, S/S, S/L, L/S) as fixed effects and controlled for dam and sire ID nested within family block as random effects. We compared this full model to reduced models by inspecting the Akaike Information Criterion (AIC). A lower AIC was obtained by excluding both cross and mass from the GLMM and so the final model consisted of only the principle component scores describing shape variation, as fixed effects.

To determine how morphologies were associated with microhabitat variables, we performed a Multivariate analysis of variance (MANOVA) using the Procrustes-aligned coordinates as the response variables and strain, stream, and sampling section were included as fixed effects. We also included a strain by section interaction term to assess if strains differed in their morphological associations to microhabitat variables. Discriminant functions grouping shape variables by stream and by stream section were subsequently estimated using the lda() function of the 'MASS' package

in R (Venables and Ripley 2002). Discriminant function scores were then plotted to visually inspect differences in morphology across streams and stream sections. A redundancy analysis (RDA) was used to ordinate each stream section's mean morphology (calculated as the mean discriminant function (DF) scores for each of the first two dimensions (i.e. DF1 and DF2) from each individual found in a stream section) as a function of the habitat variables. The mean morphology per stream section (i.e. means for the two DF dimensions for individuals within stream sections) was regressed on the mean microhabitat values for these same sections. A permutation test for RDA with 999 iterations was then calculated to test for significance of RDA axes as well as the importance of habitat variables on morphological variation. An overall permutation test for an RDA including all microhabitat variables together as well as testing for their partial effects was conducted (Legendre and Legendre 2012). Both R^2 and R^2_{adj} were calculated to account for the bias that the number of explanatory variables generates in RDA (Peres-Neto et al. 2006).

In the first part of the study, we visualized differences in morphology by first regressing U_{crit} on the Procrustes-aligned coordinates using thin-plate-splines using the TPSreg software to produce deformation grids (Rohlf and Marcus 2005). Deformation grids were then used to visualise differences in morphology based on critical swimming speeds. In the second part of the study, we visualized the differences in morphology by regressing the first RDA axis (RD1), and the second RDA axis (RD2) on the Procrustes-aligned coordinates using thin-plate-spines with the TPSreg software to produce deformation grids (Rohlf and Marcus 2005). Deformation grids allowed us to visualise how the morphologies differed as a function of habitat variables.

GLMMs were performed using the R package nlme v. 3.1-120 (Pinheiro et al. 2006). Geometric morphometrics were done using the R package 'geomorph' v. 2.1.5 (Adams and Otarola-Castillo 2013). RDA was performed using the vegan package in R (Oksanen et al. 2016). All statistical analyses were performed in R v.3.2.4 R Development Core Team (2016).

1.4 Results

1.4.1 Swimming performance

Critical swimming speed (U_{crit}) was not significantly influenced by genetic components (additive, non-additive and maternal effects) (Table 1.1). Dam ID, sire ID and the dam x sire interaction did not significantly explain variation in swimming performance in either the model which included mass and cross or the reduced models which excluded them. The estimated variance of additive, non-additive and maternal effects was low, and residual variance accounted for most of the total variance in all three models. Additive variance accounted for most of the variation attributable to the genetic components in all three models. Mass but not cross contributed significantly to swimming performance indicating that neither LaHave or Sebago nor their reciprocal hybrids differed significantly in their swimming performance. The partitioning of additive and non-additive variance also changed with the inclusion or omission of mass in the models. When mass was included, additive variance went from 13.48% to 20.01% and non-additive variance went from

5.56% to ~0.00% of the variance attributable to genetic components. This suggests that mass showed signs of being influenced by additive variance.

Table 1.1 Comparison of GLMMs used to estimate genetic effects contributing to variance in swimming performance (U_{crit}). Variance estimates include the percentage of total variance explained in parentheses.

Models	Parameters				
	Fixed effects	Random effects	Dam	Sire	Dam x Sire
1	Mass: p = 0.01 Cross: p = 0.47	Block: p = 1.00	p = 0.47	p = 0.57	p = 0.89
2	Mass: p = 0.02	NA	p = 0.37	p = 0.25	p = 0.99
3	NA	NA	p = 0.77	p = 0.54	p = 0.64

	Variance Estimates				
	Additive variance	Non-additive variance	Maternal effects	Residual Variance	Total Variance
1	0.16 (13.22%)	0.03 (2.84%)	0.02 (1.3%)	1.03 (87.58%)	1.18
2	$2.39e^{-01}$ (20.01%)	$2.08e^{-14}$ (~0.00%)	$-2.21e^{-12}$ (-1.91%)	1.03 (89.09%)	1.15
3	0.15 (13.48%)	0.06 (5.56%)	-0.01 (-1.04%)	1.05 (92.91%)	1.13

We concluded that genetic effects did not significantly contribute to variation in swimming performance and proceeded to test how morphology influenced U_{crit}. Morphology significantly influenced swimming performance (GLMM: n = 240, d.f. = 36, F = 1.60, p-value < 0.0001). Neither cross (L/L, L/S, S/L, and S/S), nor mass significantly influenced U_{crit} when we accounted for morphology in the full model (Mass: t-value = -0.72, p-value = 0.47; Cross: L/S: t-value = -0.38, p-value = 0.72; S/L: t-value = 0.47, p-value = 0.65; S/S: t-value = -1.15, p-value = 0.29). Mean U_{crit}

across all crosses was 22.93 ± 1.06 cm/s. We compared full and reduced models which included or omitted mass and cross and concluded that the best model for explaining the variance in U_{crit} was the one which only included the principal components describing the major patterns in morphological variation as fixed effects (Table 1.2). We visualized the causal relationship between morphology and swimming performance by regressing U_{crit} on the Procrustes-aligned shape coordinates using thin-plate-splines to produce deformation grids (Figure 1.1). Faster fish (higher U_{crit}) had a streamlined body shape, smaller heads relative to the rest of their bodies, and greater body and caudal peduncle depth. Slower fish (lower U_{crit}) tended to have large heads relative to their bodies, which were more slender and had a more anterior attachment of the pectoral fin.

Table 1.2 Comparison of full and reduced GLMMs describing swimming performance (U_{crit}) as a function of all the principle components of the Procrustes-aligned shape coordinates and, any extra fixed effects in the model. Random effects for all models included dam and sire ID nested within family block.

Models	Extra fixed effects	AIC
1	Cross, Mass	352.08
2	Cross	350.64
3	Mass	347.08
4	NA	345.19

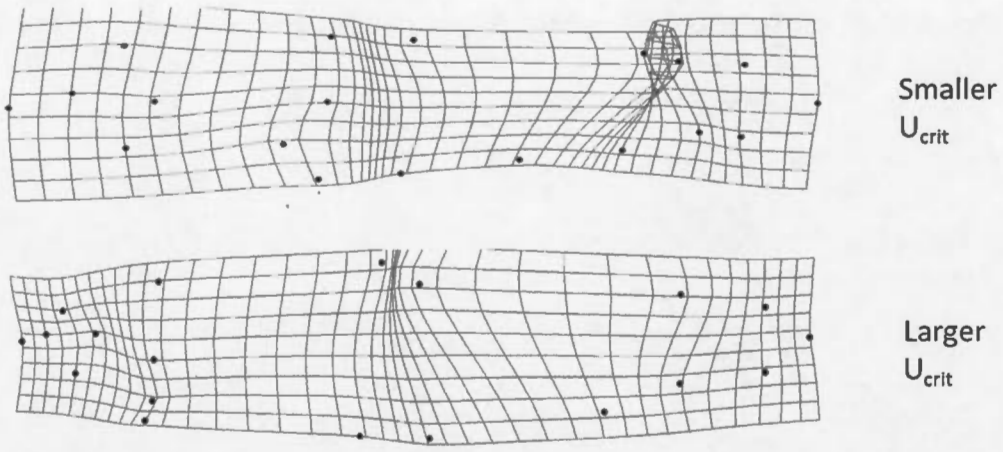

Figure 1.1 Deformation grids showing the relationship between morphology and swimming performance. Grids were obtained by regressing U_{crit}, on the Procrustes-aligned coordinates. Differences are magnified by a factor of 3.

1.4.2 Microhabitat choice

Of the 6016 parr released across all three streams, 205 were recaptured (78 in Cobourg, 49 in Duffins 1, and 78 in Duffins 2). All but 6 individuals were successfully identified to strain (LaHave = 118, Sebago = 81). Morphology was significantly influenced by fish strain, stream and stream sampling section. There was also a significant interaction between strain and stream section indicating that strains differed in their morphological matching to local microhabitat characteristics (Table 1.3). In a MANOVA, lower Wilks' λ values are indicative of a factor's greater contribution to the dependent variable's variance, and therefore stream, section and section x strain explained a large proportion of the observed morphological variation (Figure 1.2, Figure 1.3). Together the results imply that if we were to randomly sample among the individual morphologies we would be able to accurately assign

them to the stream and stream section from whence they came and to a lesser degree to their strain.

Table 1.3 MANOVA of the Procrustes-aligned shape coordinates as a function of the stream of origin, stream section and strain.

	d.f.	Wilk's λ	p-value
Strain	1	0.33	< 0.001
Stream	2	0.05	< 0.001
Section	25	$3.6e^{-04}$	< 0.001
Strain x Section	18	$7.0e^{-03}$	< 0.01

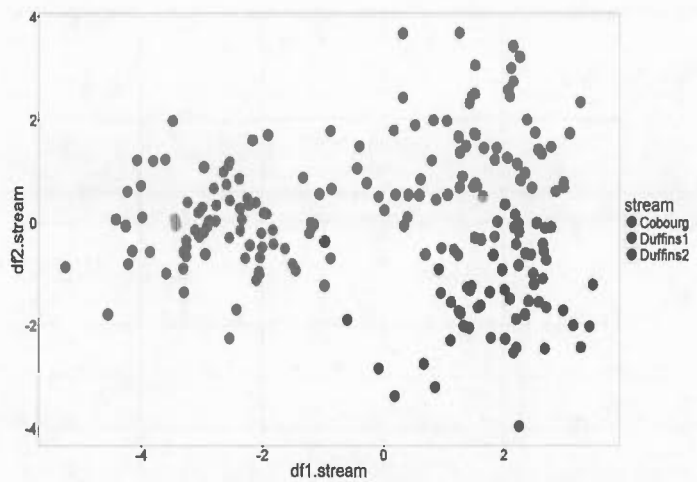

Figure 1.2 Plot of the discriminant functions (DF1 and DF2) differentiating morphological differences across streams. DF1 accounted for 81% of the variation and DF2 accounted for 19% of the variation.

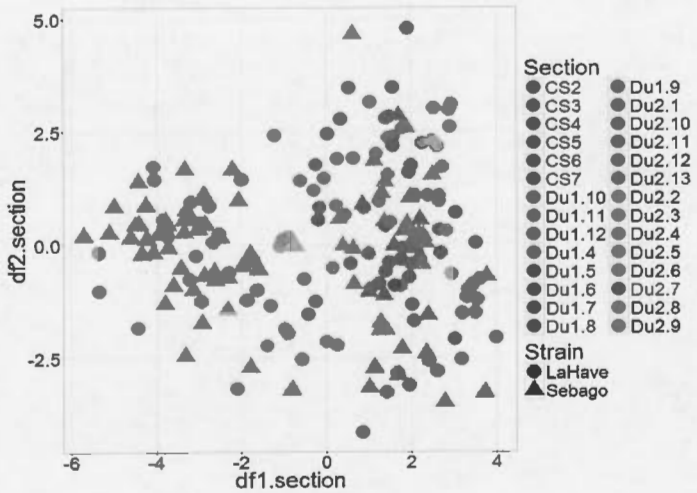

Figure 1.3 Plot of the first two discriminant functions (DF1 and DF2) differentiating morphological differences across stream sections. Each colour in the plot, referenced in the figure legend, corresponds to a different stream section (Cobourg: CS2-CS7; Duffins 1: Du1.4-Du1.13; Duffins 2: Du2.4-Du2.9). DF1 accounted for 37% of the variation and DF2 accounted for 13% of the variation.

The measured microhabitat variables significantly predicted the morphology of individuals sampled at each stream section ($R^2 = 0.64$; $R^2_{adj} = 0.46$; $p = 0.002$; Table 1.4, Figure 1.4A). Variation along RDA1 was associated with head length, body depth and concavity of the body shape as well as stream width, depth and a greater proportion of cobble (Figure 1.4A, B). Variation along RDA2 was associated with body depth, stream velocity, and proportion of silt and pebble present. Greater body depth was associated with faster water velocity.

Table 1.4 Redundancy analysis results. The mean morphology per stream section, (calculated by grouping individuals by stream section and taking the mean of the DF1 and DF2 scores of each section) was regressed onto the mean microhabitat values per stream section. The importance of components (in parentheses) and results for the permutation tests for the axes and partial effects of factors using 999 permutations are included. The full microhabitat matrix model was compared with each microhabitat characteristic specified.

Axes	d.f.	Variance	F	p-value
RDA1 (46%)	1	2.89	31.72	0.001
RDA2 (18%)	1	1.10	12.12	0.001
Terms				
Full-microhabitat	9	4.00	3.51	<0.01
Width	1	1.56	12.36	<0.01
Depth	1	0.33	2.66	0.08
Clay	1	0.36	2.84	0.06
Silt	1	0.91	7.21	<0.01
Sand	1	0.18	1.39	0.27
Pebbles	1	0.01	0.12	0.88
Gravel	1	0.19	1.46	0.26
Cobble	1	0.15	1.19	0.33
Velocity	1	0.29	2.32	0.12
Residual	18	2.28		

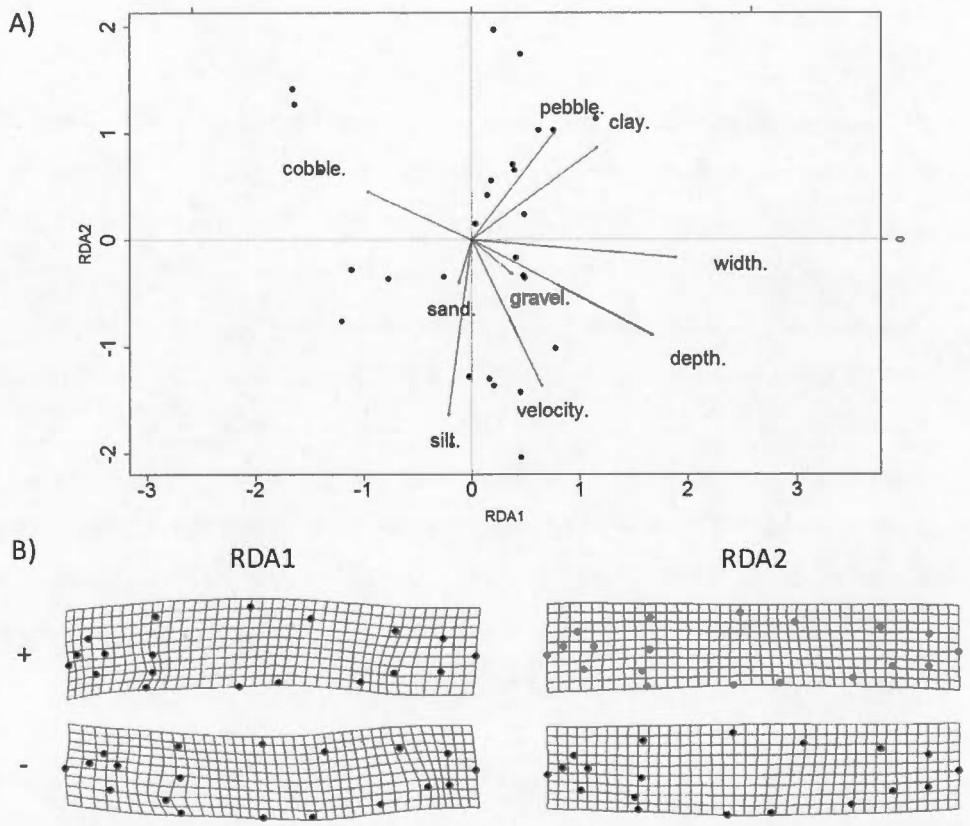

Figure 1.4 A) Redundancy analysis biplots of the mean morphology by stream section (black) on the mean microhabitat variables (blue) per stream section. B) Deformation grids showing the major patterns of shape variation across the RDA axes magnified by a factor of 3.

1.5 Discussion

We found that genetic variance had no significant effect on swimming performance for hatchery-reared Atlantic salmon parr. Furthermore, we found that individual mass did not significantly influence critical swimming speed when we accounted for morphology. There were also no significant differences in critical swimming speeds between pure half-sib families or their reciprocal hybrids. Greater critical swimming speeds were associated with streamlined morphologies and poorer swimmers were both slimmer and had relatively larger heads relative to their bodies. As all the individuals were raised in a common garden, this morphological variation may have been due to differences in competitive ability for resources among individuals (Currens et al. 1989, Rouleau et al. 2010). For the habitat choice experiment, regardless of the very low recapture success rate (~3%), we observed a significant relationship between morphology and stream microhabitat features.

1.5.1 Swimming performance

The relative contributions of genetic components to early life survival, from egg to fry, as well as other fitness related traits have been studied in great detail for both LaHave and Sebago strains (Houde et al. 2013, Houde et al. 2015a). Maternal effects were found to be important early in life but decreased over the course of development. These studies also found that the non-additive genetic variance was larger than the additive variance in early life. Few studies, however, have studied the genetic architecture of juvenile swimming performance. While we found that genetic effects did not contribute significantly to critical swimming speeds, the importance of

genetic effects may have decreased over time (Heath et al. 1999). This suggests that once juvenile Atlantic salmon reach a certain point in their ontogeny, other factors such as the environment may be more important in influencing swimming performance. In contrast, maternal effects on swimming performance have been documented in whitefish (*Coregonus clupeiformis*), clownfish (*Amphiprion melanopus*), and lake trout (*Salvelinus namaycush*) (Green and McCormick 2005, Huuskonen et al. 2009, Kekalainen et al. 2010). Dam by sire interactions also contributed significantly to swimming performance in Whitefish and Lake Trout (Kekalainen et al. 2010, Humphrey 2011). Sockeye salmon (*Oncorhynchus nerka*) on the other hand, did not show parental effects on swimming performance (Nadeau et al. 2009). Genetic effects can represent an important component of overall offspring fitness in salmonids (Robison and Lumpert 1984, Beacham 1989); however, the ontogenetic shift in the importance of genetic variance is well documented (Wangila and Dick 1996, Nadeau et al. 2009).

Pure and hybrid half-sib families did not differ significantly in their critical swimming speeds which is in contrast with Rouleau et al. (2010) who found that crosses between pelagic and littoral morphs of brook trout (*Salvelinus fontinalis*) had lower critical swimming speeds than their wild or laboratory raised conspecifics . This result that they obtained may be due to the fact that both of those morphs have very specific ecologies associated with their morphologies and hybridization led to outbreeding depression (Houde et al. 2015b, Senay et al. 2015). Hybrid crosses of wild and farmed Atlantic salmon had similar growth patterns and no significant differences in morphology (Morris et al. 2011). Similarly, hybrid striped and white bass (*Morone sp.*), showed similar growth rates and other fitness-related traits to that of their parents. Our results suggest that potential hybridization between LaHave and Sebago may not be an issue for their reintroduction to Lake Ontario where swimming

performance is concerned as they have similar critical swimming speeds when reared in a similar environment.

By the time juvenile salmonids reach the parr stage, environmental variation and differences in competitive ability may be more important to morphological and swimming performance variation than genetics (Nislow et al. 2011, Ward 2014). Our own data and other studies support this idea. For instance, juvenile perch (*Perca fluviatilis*) from two different lakes that showed morphological variation in the wild showed no differences in morphology when reared in a common garden (Heynen et al. 2009). While previous studies have documented significant additive genetic variance for fitness traits in Atlantic salmon eggs and alevins (Houde et al. 2015), our results for Atlantic salmon parr, show that most of the morphological and swimming performance variation is residual and likely caused by environmental effects. Swimming performance and morphology are plastic in salmonids and can differ drastically between populations living under different environmental conditions. Being reared in a common garden would have emphasized any individual differences as well as genetic contributions to swimming performance and morphology.

1.5.2 Morphology and microhabitat associations

Similar to other studies we found that streamlined, deeper bodied morphologies were associated with faster stream velocities (Pakkasmaa and Piironen 2001, Fu et al. 2013). We also found that the juvenile Atlantic salmon that we recaptured had morphologies that were associated to specific microhabitat variables, something that

has been observed in a number of other fish species (Wood and Bain 1995, Nislow et al. 1999, Peres-Neto and Magnan 2004). The preferred habitats of juvenile Atlantic salmon are fast flowing riffles which are associated with high levels of invertebrate drift. If their morphologies do not match that habitat, they would be unable to maintain sufficient swimming speeds to hold these high-quality territories (Finstad et al. 2011). Stream flow strongly influences the spatiotemporal distribution of fish and consequently, morphology and swimming performance limit the territories that individuals can occupy (Leavy and Bonner 2009). Morphology and microhabitat associations are not limited to salmonids but have been observed across a variety of taxa (Tulli et al. 2009, Sistrom et al. 2012, Harrison et al. 2015, Marques and Nomura 2015). The close relationship between form and ecological function in stream-dwelling fish is increasingly well documented (Wood and Bain 1995, Leavy and Bonner 2009, Senay et al. 2015).

We were also able to differentiate between the morphologies of individuals released in different streams. Juvenile salmonids have previously been noted for their morphological differentiation across different streams (Pakkasmaa et al. 1998). For instance, Solem et al. (2006) were able to discriminate between 4 wild populations of juvenile Atlantic salmon based on their morphologies. The same team later extended their study and found that they were able to discriminate between 8 wild populations of juvenile Atlantic salmon based solely on their morphologies, across three different regions of Norway (Solem and Berg 2011). Taylor and McPhail (1985), as well as Fraser et al. (2007) also noted morphological differences based on migration distances in Coho salmon (*Oncorhynchus kisutch*) and Atlantic salmon respectively. Characterizing the morphology of individuals by stream of origin and by microhabitat associations could be used by conservation authorities for identifying and targeting certain populations for protection. Comparing the ranges of morphological variations

that populations display across habitats could also be a useful tool in determining whether managing a population's phenotype is a viable form of conservation.

Together, our results provide valuable information on the variation regarding two important fitness-related traits in juvenile Atlantic salmon. By implementing controlled breeding designs and accounting for the importance in phenotypic variation post-release, supplemented stocking of salmonids may be improved. The differences in morphologies across environments that we observed are probably the result of a combination of habitat matching, phenotypic plasticity and local adaptation (Taylor and McPhail 1985, Taylor 1991, Edelaar et al. 2008, Fraser et al. 2011, Primmer 2011). While we cannot deny that some phenotype dependent mortality may have occurred, this is difficult to test for in the wild. We, therefore, cannot fully conclude that individuals made phenotype dependent habitat choices. We can argue that the individuals that we did recapture had morphologies that allowed them to initially occupy and survive in those microhabitats. Considering the morphology and swimming performance potential of populations will be an important future direction in the management of fisheries and supplemented stocking strategies of conservation management.

CHAPTER II

EFFECTS OF COMPETITION ON FITNESS RELATED TRAITS

2.1 Abstract

While interspecific competition is prevalent in natural systems we do not yet understand how it can influence an individual's phenotype within its lifetime and how this might affect performance. Morphology and swimming performance are two important fitness-related traits in fishes. Both traits are essential in acquiring and defending resources as well as avoiding predation. Here we examined if interspecific competition could induce changes in morphology and affect the swimming performance of two strains of juvenile Atlantic salmon (*Salmo salar*). We imposed competitive scenarios on the fish using artificial streams containing different combinations of four interspecific competitors. Exposure to interspecific competitors induced morphological changes over time, through the development of deeper bodies, whereas controls free of interspecific competitors, developed more fusiform body shapes. Furthermore, swimming performance was correlated to fusiform morphologies and was weaker for Atlantic salmon in competitive scenarios vs. controls. This implies that interspecific competition has direct effects on these fitness-related traits in Atlantic salmon. To the best of our knowledge, this is the first time that morphology, an important fitness-related trait linked to swimming performance, has been shown to be negatively impacted through interactions with an interspecific competitor.

2.2 Introduction

All organisms interact with their neighbours and, sufficient resources and habitat heterogeneity can produce adaptive radiation among individuals with similar niches, over generations. Phenotypic plasticity in response to different environmental conditions can, however, reduce the costs of competition within an individual's lifespan (Wiens 1989, Tilman 1994, Schluter 2000). Populations composed of individuals that have some varying degrees of morphological variation and plasticity may differ in how they perform in competitive scenarios. The relationship between competition and morphological differentiation is poorly understood despite the prevalence of interspecific competition in natural systems (Connell 1983, Fausch 1988, Miner et al. 2005). Furthermore, it is unclear whether many of the morphological differences we observe in populations are due to adaptive phenotypic plasticity or simply due to adaptive divergence over time (Grether et al. 2009).

There are few studies that examine the effects of interspecific competition on fitness-related traits during the course of an individual's lifetime (Miner et al. 2005, Grether et al. 2009, Nislow et al. 2011). There is, however, a rich literature on ecological character displacement where niche partitioning and adaptive radiation between two or more species living in sympatry have already occurred (Schluter 1994, Schluter 2000). For example, Melville et al. (2002) surveyed two species of alpine lizards and found that the differences in their size and competitive ability were greater when living in sympatry, but not in allopatry and that the smaller of the two was forced into less favourable habitats. Similarly, Adams (2010) analysed the skull morphology of two species of terrestrial salamanders and found that both species had more robust skulls, characterised by differences in skull size, jaw length and jaw thickness, when

living in sympatry but not in allopatry. Robust skulls were also correlated with aggressive behaviour and Adams hypothesized that both of these traits should give a competitive advantage in interspecific interactions. The problem with this approach is that these character shifts may be masked when the phenotypic variation is associated with an environmental gradient or under spatial autocorrelation (Goldberg and Lande 2006, Adams and Collyer 2007). One way to overcome these potentially confounding factors is to manipulate competition in a controlled environment. The goal of this study was, therefore, to investigate if interspecific competition, in a controlled environment, could impact individual performance by modifying individual morphology within an individual's lifetime. We used an ecologically and economically important species for our investigation, the Atlantic salmon (*Salmo salar*).

Salmonids are good models for experimentation as they can rapidly respond to changes in the abiotic and biotic environment by adaptively modifying their behaviour, physiology, and development (Fausch 1998, Hutchings 2004, Fraser et al. 2011). Both morphology and swimming performance are important, easily measurable, traits for resource acquisition, territory defence, and predator avoidance and are good indices for fitness in fish (Plaut 2001, Álvarez and Metcalfe 2007, Rouleau et al. 2010, Colborne et al. 2011). Given that form follows function, morphology and swimming performance are tightly associated in salmonids (Blake 2004). For example, shallower, streamlined, fusiform body shapes are important for juvenile Atlantic salmon as this hydrodynamic morphology reduces drag and the energetic costs of swimming. As juvenile Atlantic salmon preferentially establishes territories in fast flowing riffles, individuals with a fusiform body shape would have an advantage over individuals with less hydrodynamic morphologies (Taylor and McPhail 1985, Leavy and Bonner 2009, Finstad et al. 2011). Deeper body shapes, on

the other hand, allows individuals to achieve greater acceleration, improved burst swimming performance, and greater manoeuvrability in complex habitats, all of which are essential for foraging and predator avoidance (Blake 2004, Domenici et al. 2008). Perceived body size is also a common predictor of competitive ability and dominance in fish. Individuals with deeper bodies and a larger profile will be perceived as having a greater size which may reduce antagonism from interspecific interactions regardless of actual size (Huntingford et al. 1990, Ward 2006). Atlantic salmon also provide a good system for studies on interspecific interactions as they face severe competition from introduced non-native species in the North American Great Lakes. Atlantic salmon's main competitors in the Great Lakes include brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*) (Crawford and Muir 2007; Nislow et al. 2011). These non-native species are ecologically similar to Atlantic salmon but have not evolved together, and as such, have the potential to be strong competitors for similar resources and territory These competitors are also known to impact Atlantic salmon fitness by decreasing their social status, increasing their energy expenditure, and increasing their stress levels (Scott et al. 2005a, Scott et al. 2005b, van Zwol et al. 2012a, Van Zwol et al. 2012b).

Morphology and swimming performance are often plastic in a salmonid's lifetime, and variation in both of these traits is often associated with an abiotic environmental gradient, such as water velocity (Pakkasmaa and Piironen 2001, Peres-Neto 2004). While Atlantic salmon are plastic for a number of life-history traits (Klemetsen et al. 2003), and intraspecific competition has been studied extensively in this species, few studies have addressed how the biotic environment (e.g. interspecific competition) can induce a plastic response in fitness-related traits (Fausch 1998, Grether et al. 2009, Nislow et al. 2011). There is already some evidence that biotic interactions

such as predation can induce plastic morphological responses in fishes. For example, developing a deeper body is a form of inducible morphological defence in prey fishes which are exposed to the risk of predation (Chivers et al. 2007). Not only will gape-limited predators preferentially eat shallow-bodied prey, they might also cause individuals to change their habitat use, removing them from the fast flowing water which induces fusiform body shapes in salmonids (Pakkasmaa and Piironen 2001, Fu et al. 2013). Similarly, this may put a great selective pressure for morphological plasticity on individuals to develop deeper body shapes in the presence of competitors and fusiform body shapes in the absence of competitors (Harvell 1990, Chivers et al. 2007, Grether et al. 2009, Leavy and Bonner 2009). While this change in morphology may be adaptive in the presence of competitors, it could result in a trade-off with swimming performance as any change in morphology may have a strong effect on the hydrodynamic forces experienced by an individual (Pettersson and Brönmark 1997, Blake 2004, Fu et al. 2013). We hypothesized that strong interspecific competition can induce morphological plasticity which in turn will impact swimming performance. This relationship may be analogous to the morphological changes and swimming performance trade-offs experienced by individuals under the risk of predation (Van Buskirk and Relyea 1998, Relyea 2000, Grether et al. 2009).

To test for the effects of interspecific competition on fitness-related traits important in the early life of Atlantic salmon; we set out a comprehensive experiment to test whether the four aforementioned interspecific competitors could affect Atlantic salmon morphology and swimming performance in controlled artificial streams. Two strains of juvenile Atlantic salmon were compared during this study: the LaHave strain from Nova Scotia and the Sebago strain from Maine. An additional benefit to using these strains as our study species is that both are candidate strains for a Canadian government funded Atlantic salmon reintroduction program in the Great

Lakes (Huntsman 1944, Netboy 1968, Diamond and Smitka 2005) and information regarding their performance when faced with competition is of great importance to the reintroduction effort. If interspecific competition with Atlantic salmon is able to influence these two traits, then individual fitness of these stocked strains will be impacted in the wild (Finstad et al. 2011), and impede self-sustaining populations from forming (Fausch 1988, Fausch 1998). We predicted that individual morphology would be influenced by interspecific competition and that this relationship would vary as a function of the interspecific competitor as they could impose different degrees of competitive pressure on Atlantic salmon. We also expected that swimming performance and morphology would be highly correlated, but that interspecific competition may impose a trade-off that affects individual swimming performance.

2.3 Materials and methods

2.3.1 Subjects

Juveniles of all salmonid species were provided by the Ontario Ministry of Natural Resources (OMNR). Fertilised eggs from single-pair matings of wild LaHave (LaHave River, Nova Scotia, Canada: 44°14′N64°20′W) were received from 1989 to 1995, and captive generations were produced every year in Ontario starting in 1996. Fertilised eggs from single-pair matings of wild Sebago in Panther River (A tributary of Lake Sebago, Maine, U.S.S.: 43°53′N, 70°27′W), a hatchery-supplemented river, were received in 2006. Families for both strains of this experiment were produced in early November 2010 at the OMNR Harwood Fish Culture Station. For each strain, we randomly selected mature adults for a blocked full factorial 5x5 North Carolina

breeding design (Lynch and Walsh 1988). Fertilised eggs were then transported the same day as fertilization to the OMNR Codrington Fisheries Research Facility for rearing.

Rainbow trout and brown trout were produced from hatchery parents derived from the Ganaraska River, Ontario. Chinook salmon and Coho salmon were produced from wild parents from the Credit River, Ontario. The fry of each species were kept in tanks (38 L, $n = 250$ fry) at the Codrington Facility until used in the artificial streams. Although the species differed slightly in initial body length (LaHave: 5.8 ± 0.4 cm; Sebago: 5.6 ± 0.5 cm; brown trout: 6.0 ± 0.7 cm; rainbow trout: 6.0 ± 0.6 cm; Chinook salmon: 8.2 ±0.7 cm; Coho salmon: 8.5 ± 1.0 cm), the juveniles of each species were the same age and thus representative of interspecific intra-cohort competition that would occur in a natural setting. Greater details on the non-native competitor populations can be found in Houde *et al.* (2015).

2.3.2 Experimental procedures

Artificial streams were constructed at the Codrington Facility, Ontario, Canada. The artificial streams measured 2.4 m long by 0.25 m wide and the bottom was lined with gravel and pebbles creating a semi-natural environment The artificial stream was openly divided into a riffle section characterised by shallow, fast flowing water (1.60 m long, 0.25 m wide, and 0.40 m deep), and a pool section characterized by deeper, slower moving water (0.8 m long, 0.25 m wide and 0.80 m deep). . These were included in the design of the streams as they are the preferred habitats of juvenile salmonids (Arnold et al. 1991; Finstad et al. 2011). Natural stream water was actively

pumped through the experimental streams at a flow rate between 0.41 $m \cdot s^{-1}$ in the riffle section at the headwater and 0.27 $m \cdot s^{-1}$ in the pool section downstream, measured using a 10 second average for each point using a digital flowmeter (Höntszsch, Germany);. Both stream velocities were representative of velocities experienced by juvenile salmonids in the wild (Keeley and Grant 1995). Fish were exposed to natural fluctuations in stream temperature and photoperiod. Throughout the experiment, the fish were fed commercial pellets once daily at a quantity of 3% total body mass. For more detailed information on the artificial streams and experimental setup consult the supplementary material of Houde *et al.* (2014).

Individual LaHave and Sebago, as well as the competitor species, were randomly assigned to one of seven experimental treatments beginning in September 2011 and lasting for a total of 45 weeks, ending in August of 2012 (Table 2.1). Each treatment had two replicates which were run in tandem. Initial fish density was kept at a constant of 32 fish per stream. These higher than natural densities were used to encourage competitive interactions (Steingrímsson and Grant 1999).

Prior to being placed in the artificial streams in September, 2011, a subset of Atlantic salmon (n = 240) were lightly anesthetized (MS-222), removed from the water, weighed on a digital scale, and had their left sides digitally photographed next to a measuring scale Immediately following this, the fish were placed in fresh stream water with an oxygen bubbler to recover. Once recovered and swimming freely, the fish were returned to the artificial streams. This was repeated another three times throughout the study (2^{nd} sample after 5 weeks, 3^{rd} sample after 36 weeks, and 4^{th} sample after 45 weeks; Table 2). As intraspecific and interspecific competition for refuges is high in the winter, measuring was avoided during this time so as not to

further encumber survival (Harwood et al. 2002). Nineteen homologous landmarks (Fig. 1) were placed on each digital photograph using the tpsDig2 software (Rohlf and Marcus 2005). The homologous landmark coordinates were then analyzed using a generalised Procrustes analysis and subsequently transformed into partial warps which are used to compare morphologies using subsequent multivariate analyses (Zelditch et al. 2004). These shape variables were then contrasted across treatments and strains (see statistical analyses below).

We measured the critical swimming speed, an estimate of the maximum sustained speed which is an exclusively aerobic activity, and burst swimming speed, an anaerobic form of swimming where the highest levels of exercise performance are attained (Beamish 1978; Domenici and Blake 1997; Peake et al. 1997; Peake 2008). Both were measured on the same subset of Atlantic salmon after 10 months of exposure to the interspecific competitors. ($n = 135$; 8 per treatment; however due to mortalities and individuals being set aside for a parallel study (Houde et al. 2015) some treatments had smaller sample sizes). Each fish was measured first for burst swimming speed then after a > 10-minute recovery; the critical swimming speed was measured. Swimming performance was not measured multiple times in individuals to avoid stress and decrease the possibility of mortality. Burst swimming speed was measured in an acrylic raceway (25 cm x 23 cm x 150 cm), filled to a depth 15 cm of water. Individuals were confined to one end of the raceway with a plastic barrier and a shelter was placed at the other end to encourage directed swimming. After acclimating for 5 minutes, the barrier was removed and the individual was immediately exposed to a simulated predation event (golf ball being dropped from a distance of 50 cm directly overhead of the individual), causing a swimming escape response towards the far end of the raceway (Colborne et al. 2011; Lima and Dill 1990; Peres-Neto and Magnan 2004). Where fish were unresponsive to the golf ball

stimulus, the handle of a fish net was used to gently probe the caudal fin to elicit swimming. If fish were still unresponsive to this stimulus, they were removed from the experiment but were still used in the critical swimming speed assay. Trials were recorded with a high-speed camera at 60 frames per second (Fastec Imaging) and video tracking software (Kinovea v. 0.8.15) was used to calculate the maximum burst swimming speed achieved. This was calculated as the maximum instantaneous velocity of the head of the fish between each frame in the video.

Critical swimming speed was measured using an acrylic swim flume (Loligo Systems, Denmark). Following the burst swimming speed trial, the Atlantic salmon were then placed individually into the swim chamber and left to acclimate for 10 minutes. Water velocity was then increased by approximately 0.19 cm/s every 2 minutes until the fish showed signs of fatigue. Fatigue was defined as when a fish could no longer actively swim against the current and was swept back against the mesh at the back of the chamber even after a single, mild (5-10V) electric pulse was administered to elicit movement. Critical swimming speed (U_{crit}) was calculated as $U_{crit}=U_i + (T_i/T_{ii} \text{ X } U_{ii})$ for each individual (Plaut 2001), where *Ui* is the highest velocity maintained for a full 2 minute interval, *Ti* is the time of fatigue at last current velocity (minute), *Tii* is the interval length (2 minutes), and *Uii* is the water velocity increment (0.19 $m \cdot s^{-1}$). While many variations of this protocol exist, they are typically designed for adult fish and so shorter time intervals were used to better reflect the stream environment of juvenile Atlantic salmon where there are daily and seasonal fluctuations in water velocity (Peake 2008, Tierney 2011).

2.3.3 Statistical analyses

Two-way multivariate analysis of covariance (MANCOVA) was used to test for differences in partial warp scores (i.e., shape differences) across treatments and strains for each of the four sampling periods. Treatment and Atlantic salmon strain were used as fully interacting fixed effects in the model. Fish were not individually marked so a repeated measures model was not feasible. Although partial warps, generated from a generalised Procrustes analysis, are standardized for scale, orientation and position within the digital photograph, we also tested how final mass differed across treatments and strains as an additional estimate as to how interspecific competition could influence individual growth. We assessed this using a two-way ANOVA with treatment and strain as interacting fixed effects and artificial stream ID as a random effect.

To compare how treatments and strains differed in shape, we used discriminant function analysis (DFA) using the "MASS" package in R (Venables and Ripley 2002, Ripley et al. 2015), and thin-plate splines (Bookstein 1991). DFA was used to determine which shape variables (partial warp scores) predicted membership to a particular group (strain and treatment). We calculated the first two discriminant functions for each strain's morphology across treatments separately to focus on the effects of interspecific competition on morphology. We tested the significance of these relationships for each discriminant function using a one-way ANOVA with treatment as a fixed effect and posthoc pairwise t-test with a Bonferroni correction. The main patterns of shape differentiation across treatments and strains were visualized using thin-plate splines produced by regressing each multivariate partial warp score onto each of the discriminant functions. Deformation grids were then produced using the tpsRegr software (Rohlf and Marcus 2005).

Two-way ANCOVAs were used to determine how burst swimming speed and critical swimming speeds differed across treatments and strains. As above, treatment and Atlantic salmon strain were used as fully interacting fixed effects in the model and mass was included as a covariate. A posthoc Tukey test was then used to compare swimming performances among groups when statistical differences were found.

Finally, we used Pearson's correlation coefficient to test whether individual morphology (discriminant functions for each strain) were correlated to swimming performance and whether burst and critical swimming speeds were correlated. All morphological analyses were done with the tps software suite (Rohlf and Marcus 2005). All statistical tests were done with R v. 3.02 (R core team (2014).

2.4 Results

2.4.1 Morphology

Significant differences between the morphology of the strains were apparent from the beginning of the experiment (MANCOVA: Wilks $\lambda = 0.40$, $n = 240$, $P < 0.001$) and persisted throughout the rest of the experiment (Table 2.1). LaHave had significantly shorter, blunter heads, whereas Sebago had more elongated heads resulting in a more streamlined body shape (Figure 2A, B, Table 1).

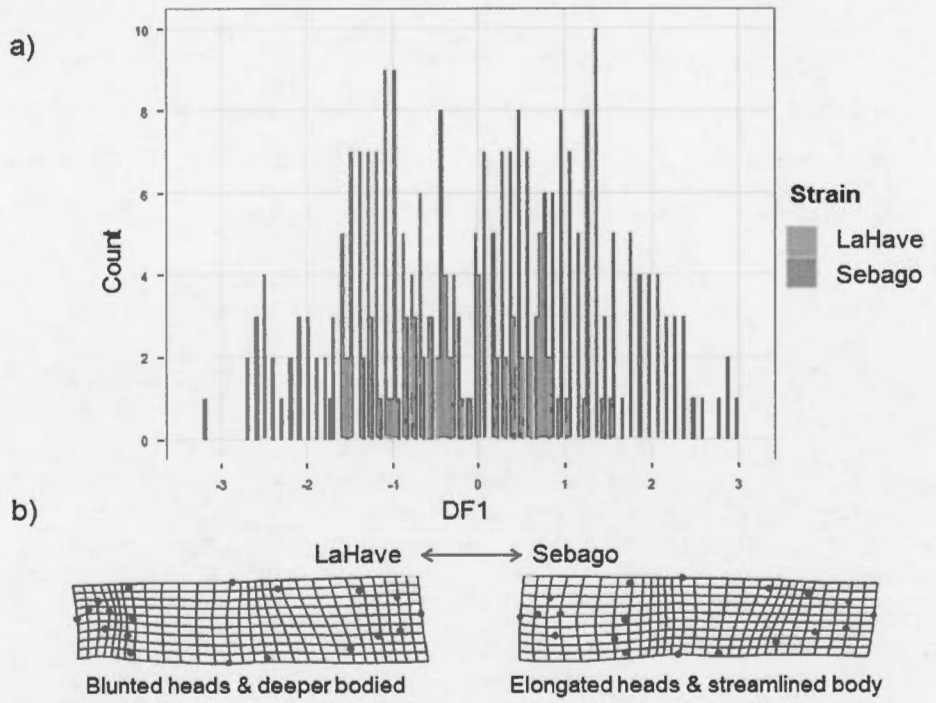

Figure 2.1 A): a) Barplot of the discriminant function scores for the final sample (45 weeks), showing differences between the morphologies of the two strains of Atlantic salmon: LaHave and Sebago. b) Thin-plate splines were used to visualize the differences in shape between the two strains.

There were significant morphological differences across the interspecific competition treatments. These differences appeared after 36 weeks but were also influenced by the strain of the individual. These differences persisted to the final (45 weeks) sampling period where they were more accentuated (Table 2.1; Figures 2.2, 2.3). Both Sebago and LaHave salmon varied in shape similarly, developing a deeper body shape in the presence of inter- or intraspecific competitors of the opposing strain, while tending towards a streamlined shape in the absence of these competitors (Figures 2.2, 2.3). However, only control treatments of Sebago had significantly distinctive streamlined shape when compared to other treatments (Figure 2.2). Individuals from both strains

paired with brown trout had the deepest body shapes of all. Individuals paired with Chinook salmon or rainbow trout were the most similar in morphology to the control treatments whereas individuals paired with Coho salmon and in the multi-species mixed treatment and the intraspecific competition treatments (LaHave and Sebago) were slightly less streamlined than the control treatment.

Table 2.1 Differentiation of morphologies among strains and treatments taken throughout the experiment. Partial warps were used as the response variables in a MANOVA test to test for significance among treatments and strains (N.A.s in the initial sample due to the fish being measured before being placed in a treatment). Numbers in parentheses indicate the sample size.

Samples	Strain		Treatment		Interaction	
	λ	*P*	λ	*P*	λ	*P*
Initial (240)	0.40	<0.001	N.A.	N.A.	N.A.	N.A.
5 weeks later (240)	0.35	<0.001	0.94	0.64	0.43	0.70
36 weeks later (442)	0.47	<0.001	0.19	<0.001	0.29	<0.001
45 weeks later (312)	0.55	<0.001	0.20	< 0.001	0.32	< 0.001

Overall, the control treatment of LaHave salmon had less distinctive morphologies from the competition treatments than did their Sebago counterparts. In contrast to Sebago, control treatments of LaHave salmon were not the most streamlined treatment, resembling individuals paired with Rainbow trout and Chinook salmon in morphology. Individuals paired with Coho salmon and in the mixed treatment had deeper bodies. LaHave salmon paired with brown trout had too few survivors to include in the analysis.

The final masses of Atlantic salmon differed across treatments. Treatments, where Atlantic salmon were paired with either rainbow trout or brown trout, had a significantly lower mass than all other treatments. Mortalities were also very low, occurring only after the 36-week point in treatments containing rainbow trout or brown trout (but see (Houde et al. 2015c)).

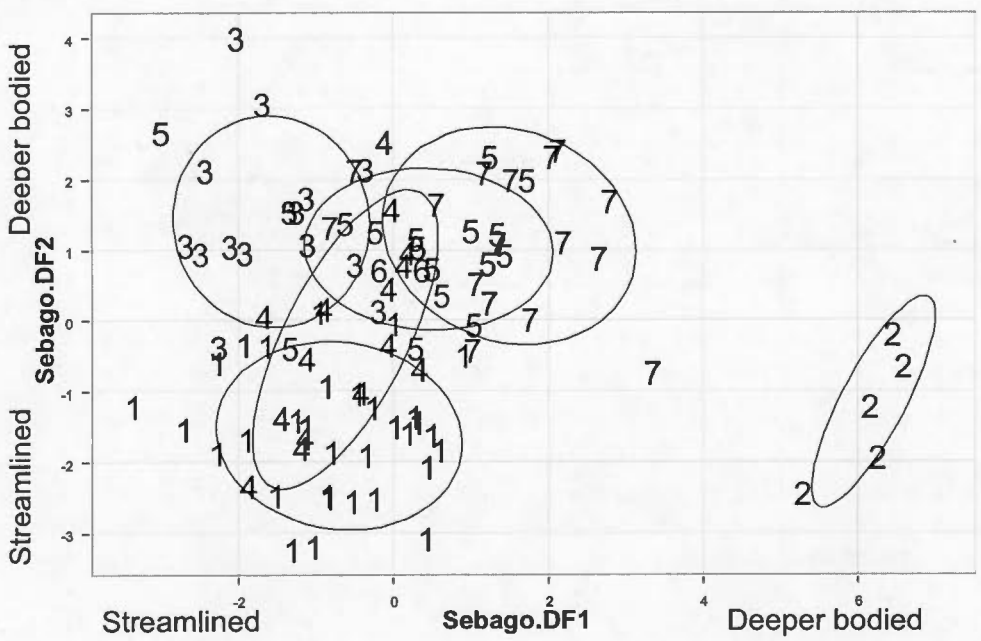

Figure 2.2 Scatterplot of the discriminant functions (DF1 and DF2) describing differences in morphology by treatment for Sebago: 1) Sebago only, 2) brown trout, 3) rainbow trout, 4) Chinook salmon, 5) Coho salmon, 6) Mix and 7) LaHave-Sebago. 95% Confidence ellipses were calculated to assist in distinguishing between group differences.

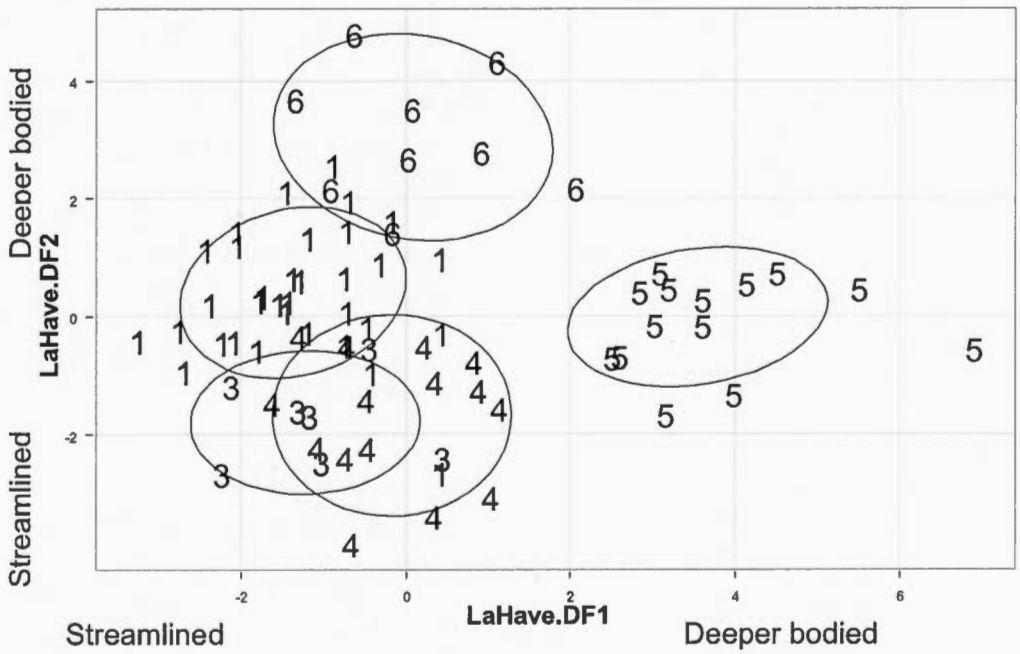

Figure 2.3 Scatterplot of the discriminant functions (DF1 and DF2) describing differences in morphology by treatment for LaHave: 1) Sebago only, 2) brown trout, 3) rainbow trout, 4) Chinook salmon, 5) Coho salmon, 6) Mix and 7) LaHave-Sebago. 95% Confidence ellipses were calculated to assist in distinguishing between group differences. The absence of brown trout treatment (2) was due to mortalities.

2.4.2 Swimming performance

Burst swimming speeds (1.23 cm/s ± 0.35 cm/s) did not differ significantly between treatments (ANOVA: $F = 0.47$, $P = 0.83$) or strains ($F = 1.34$, $P = 0.25$) and was not correlated to mass ($r = 0.17$, $P = 0.07$) or critical swimming speed ($r = 0.12$, $P = 0.18$; Table 2.2).

Critical swimming speeds were correlated to mass ($r = 0.27$, $P < 0.01$) which was subsequently included as a covariable in all subsequent analyses. Considering both strains together, control groups had a mean critical swimming speed of 83.15 cm/s *vs.* 55.09 cm/s in treatments with interspecific competitors. When controlling for individual mass, these differences in critical swimming speeds between treatments were significant (ANOVA: $F = 6.28$, $P < 0.001$) but not between strains (ANOVA: $F = 0.24$, $P = 0.63$). There was, however, a significant interaction between strain and treatment (ANOVA: $F = 2.89$, $P < 0.05$). To further look into differences between strains, LaHave and Sebago salmon were split for subsequent analyses. We observed no significant differences in critical swimming speeds among treatments for LaHaves, suggesting interspecific competition did not seem to affect swimming performance (ANOVA, $F = 1.19$, $n = 64$, $P = 0.32$; Figure 2.4). On the other hand, critical swimming speeds did differ significantly among treatments for Sebago (ANOVA, $F = 7.48$, $n = 75$, $P < 0.001$; Figure 2.4, Table 2.2). A posthoc Tukey-Kramer test revealed that control treatments of Sebago salmon as well as Sebago in the intraspecific competition treatment had significantly greater critical swimming speeds than all other treatments with an interspecific competitor (Figure 2.4, Table 2.2). Swimming performance did not depend on which species of competitor was present. Critical swimming speed in the intraspecific competition treatment was significantly different from controls for LaHave but not for Sebago, although their critical swimming speeds were both lower when compared to controls (LaHave control: 70.41 ± 26.10 cm/s *vs.* intraspecific competition: 67.53 ± 16.93 cm/s; Sebago control: 95.89 ± 23.30 cm/s *vs.* intraspecific competition: 71.96 ± 17.51 cm/s.

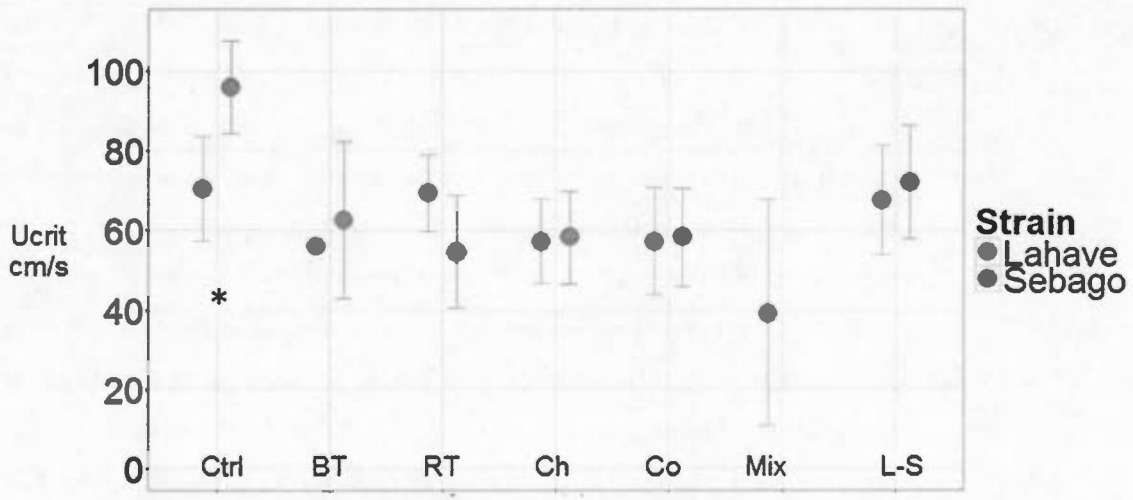

Figure 2.4 Means and 95% confidence intervals for the critical swimming speeds (U_{crit}) of Atlantic salmon by strain and treatment. (Ctrl = Control, BT = brown trout, RT = rainbow trout, Ch = Chinook salmon, Co = coho salmon, Mix = all four interspecific competitors, and L-S = LaHave-Sebago. ANCOVAs were used to test for differences among treatments. Statistical significance is indicated by (*). Mortalities in the LaHave-Brown trout and Sebago-Mix treatments prevented means and confidence intervals from being calculated.

Table 2.2 Experimental design showing results for the means and standard deviations of the final mass and fork length taken for each strain and treatment group as well as the critical swimming speed (U_{crit}) and burst swimming speeds taken from a subset of these Atlantic salmon; (n = 8 per replicate). (Numbers between parentheses are combined sample size for both replicates; # denotes mortalities)

Treatment	Ratio AS: Competitor	Strain	Final mass (g)	Final Length (cm)	U_{crit} (cm/s)	Burst (m/s)
Control	32:0	LaHave (16)	21.42±7.34	11.98±1.49	70.41±26.10	1.25±0.39
		Sebago (16)	22.26±7.22	12.35±1.60	95.89±23.30	1.12±0.45
Brown trout	16:16	LaHave (1)	14.91	10.95	56.01	1.05
		Sebago (6)	15.23±4.11	10.50±0.37	62.50±24.07	1.30±0.23
Rainbow trout	16:16	LaHave (12)	15.98±4.57	10.86±1.06	69.21±16.77	1.43±0.33
		Sebago (11)	15.94±3.00	10.98±0.90	54.49±23.48	1.05±0.30
Chinook salmon	16:16	LaHave (16)	20.35±6.94	12.12±1.73	57.15±21.25	1.22±0.19
		Sebago (16)	20.37±7.41	12.31±1.97	58.10±23.27	1.19±0.36
Coho salmon	16:16	LaHave (10)	23.61±11.53	11.62±1.45	57.15±21.26	1.25±0.43
		Sebago (14)	26.38±13.07	11.83±1.57	58.10±23.24	1.29±0.24
Mix	16:4:4:4:4	LaHave (3)	17.23±7.56	10.95±1.30	39.11±24.62	1.02±0.13
		Sebago (2)	28.33±1.95	13.35±0.21	#	#
LaHave-Sebago	16:16	LaHave (6)	25.46±10.39	11.91±1.66	67.53±16.93	1.22±0.35
		Sebago (6)	16.47±7.59	11.88±2.25	71.96±17.51	1.40±0.45

2.4.3 Morphology and swimming performance

Differences in morphology between strains and treatments were also significant within the subset of fish that were measured for swimming performance (MANOVA: Treatment: Wilks $\lambda = 0.47$, $n = 133$, $P < 0.001$; Strain: Wilks $\lambda = 0.03$, $n = 133$, $P < 0.001$; Interaction: Wilks $\lambda = 0.05$, $n = 133$, $P < 0.001$).

Considering both strains together, we found that across all treatments, critical swimming speed (Ucrit) was correlated to shape. More specifically, the first

discriminant function describing shape across treatments (DF1-treatment, representing 42% of shape variation) was correlated with Ucrit ($r = 0.30$, $P < 0.001$) but not the second discriminant function (DF2-treatment, representing 23% of shape variation; $r = 0.11$, $P = 0.19$). Burst swimming speed, however, was not correlated to shape (DF1-treatment: $r = 0.07$, $P = 0.43$; DF2-treatment: $r = -0.05$, $P = 0.56$).

We decided to treat each strain separately because it was determined that there was a significant interaction term between strain and treatment for critical swimming speeds (ANCOVA: $F = 4.12$, $P = 0.04$). For Sebago salmon, the first discriminant function (DF1-Sebago) described 39% and the second function (DF2-Sebago) described 29% of the morphological variation among treatments. We found that body shape (DF2-sebago but not DF1-sebago), which ranged from a deeper bodied morphology to a more shallow, streamlined morphology, was correlated to critical swimming speed ($r = 0.48$, $P < 0.001$; Figure 2.5), but not to burst swimming speed. For LaHave salmon, the first discriminant function (DF1-LaHave) described 38% and the second function (DF2-LaHave) described 29% of the morphological variation. Neither discriminate function (DF1-lahave or DF2-lahave) was correlated to the swimming performance measures.

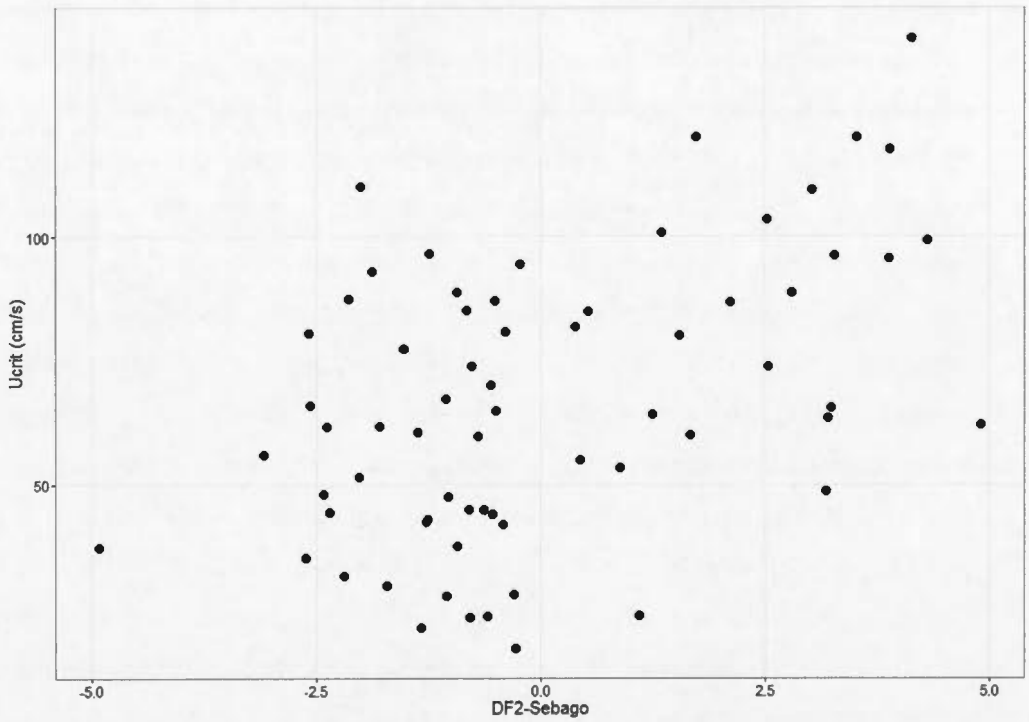

Figure 2.5 Scatter plot showing the relationship between critical swimming speed (U_{crit}) and morphology (DF2-Sebago). A Pearson product moment coefficient test indicated a significant positive relationship ($r = 0.48$, $p < 0.001$)

2.5 Discussion

To the best of our knowledge, this is the first time anyone has directly sought to experimentally measure the effect of interspecific competition on individual morphology and performance in fish. Our results indicate that interspecific competition can induce morphological differentiation in juvenile Atlantic salmon within a matter of months and that this, in turn, impacts swimming performance. These results are similar to studies which examined trait-mediated indirect

interactions in multi-species food webs. While these studies focussed primarily on how the presence of a predator could induce morphological change in prey species, they also unexpectedly found that in the absence of predation, competition between the two prey species, or two morphs of the same species, could still lead to changes in morphology. These morphological changes led to trade-offs between their competitive ability and their vulnerability to predation (Harvell 1990, Werner and Peacor 2003). For example, Van Buskirk & Relyea (1998) found that in the absence of predators, tadpoles of the wood frog (*Rana sylvatica*) that had shorter bodies and deeper tails (inducible defenses against predation) were poorer competitors and had poorer survival when compared to individuals that did not develop that morphotype. Similarly, in the absence of predators, competition between wood frog and leopard frog (*R. pipiens*) tadpoles resulted in changes in mouth width and tail length when housed together but not when reared separately. This could lead to differential foraging success between the two species and supports the idea that competition can alter morphology (Relyea 2000). Along with our own results, these studies support the argument that competition can induce a generalised, plastic, morphological response (Grether et al. 2009).

In this study, interspecific competition induced a deeper, less fusiform morphology as well as a lower $U_{crit,}$ indicative of a poorer swimming performance (Tierney 2011), in juvenile Atlantic salmon. Fusiform morphologies were correlated to swimming performance, implying that there was a cost to developing a deeper body shape in response to competition. Our results are similar to the changes in morphology observed across a wide variety of taxa when inducible defences are developed by prey species in response to the risk of predation (Chivers et al. 2007; Harvell 1990). This further suggests a generalised morphological response to antagonistic interactions with other species (Grether et al. 2009). As opposed to a direct

antagonistic interaction, the interspecific competitors could be causing a shift in habitat use in the Atlantic salmon which could have exposed them to different environmental factors such as slower water currents. Faster water currents found in riffles, the preferred habitat of juvenile Atlantic salmon, are known to induce fusiform body shapes in salmonids (Fu et al. 2013; Pakkasmaa and Piironen 2001). It is unclear whether developing a deeper morphology would be advantageous in a natural environment with interspecific competitors present but it is clear that swimming performance is impacted through the development of a deeper body. These results are therefore important in understanding how Atlantic salmon reintroductions in streams where non-native competitors are present can potentially impact the swimming performance of individuals and could lead to a decrease in fitness.

2.5.1 Differences in morphology

The differences in morphology were not initially present but developed over the course of the experiment. This suggests that these changes were induced by the presence of interspecific competitors or through some mechanism of interference competition. The difference in final masses among groups relative to controls suggests that interference competition is at play. Individuals in treatments containing Brown trout and rainbow trout were significantly smaller (Houde et al. 2014). Indeed the two groups with mortalities are those containing brown trout and rainbow trout suggesting that the smaller individuals that remained may have been able to avoid antagonistic interactions (or predation) by taking refuge in the interstitial spaces provided by the rocky substrate of the artificial streams, which the larger individuals could not do (Harwood et al. 2002). This makes sense as both brown trout and

rainbow trout are known to have negative effects on the fitness of Atlantic salmon (Scott et al. 2005a, Scott et al. 2005c, Nislow et al. 2011, Hasegawa 2016).

Interspecific competition was sufficient to induce morphological change in Atlantic salmon because the differences in morphology across treatments that we observed developed due to prolonged exposure to the interspecific competitors. Furthermore, Atlantic salmon developed different morphologies as a function of the interspecific competitor with which they were paired. Brown trout and rainbow trout appeared to induce the greatest departure from control treatments where fusiform body shapes were the norm., though both of these species induced different morphologies in Atlantic salmon. Each treatment of Atlantic salmon in competition treatments differed significantly in at least one of the discriminant functions describing shape variation from control morphologies. Not only did morphology vary across treatments but the difference in final masses among groups relative to controls suggests that interspecific competitors had a negative impact on Atlantic salmon. The interspecific competitors could have influenced Atlantic salmon mass by either acquiring more food resources themselves or directly impeding the Atlantic salmon from feeding. Indeed, interference competition whereby the non-native competitors antagonize Atlantic salmon and keep them from directly acquiring resources could explain why the final masses of Atlantic salmon in treatments containing brown trout and rainbow trout were significantly smaller (Houde et al. 2015). Indeed, the groups with a greater number of mortalities are those containing brown trout and rainbow trout, suggesting that the smaller individuals that remained may have been able to avoid antagonistic interactions (or predation) by taking refuge in the interstitial spaces provided by the rocky substrate of the artificial streams, which the larger individuals could not do (Harwood et al. 2002). This makes sense as both brown trout and rainbow trout have

negative effects on the fitness of Atlantic salmon (Scott et al. 2005a, Scott et al. 2005b, Nislow et al. 2011).

The differences in body shape that we observed between strains were present from the onset of the experiment. This result is consistent with other studies which have observed differences between the morphologies of different populations of salmonids. For instance, Solem and Berg (2011) were successfully able to correctly discriminate between eight populations of juvenile Atlantic salmon from three different regions in Norway as well as the river of origin by looking at morphology. Since both strains were raised in the same environmental conditions from birth, and are several generations removed from wild populations, these divergent morphotypes could represent variation for morphological plasticity between these Atlantic salmon strains in response to their environments (Fraser et al. 2011). For example, wild populations of salmonids found in the same river vary in morphology as a function of the distance they have to migrate. Populations with greater distances to migrate tend to be more fusiform than populations with shorter distances to travel. This hydrodynamically streamlined morphology could be adaptive as it would reduce the costs of locomotion (Taylor and McPhail 1985, Fraser et al. 2007).

2.5.2 Differences in swimming performance

Our observed values for critical swimming speeds fell within the published ranges documented for the species at the parr life-stage (Peake 2008). Our results suggest that while falling within accepted norms for the species and life stage (Peake 2008), critical swimming speeds in Atlantic salmon were lower in the presence of

interspecific competitors. If interspecific competitors were directly antagonising Atlantic salmon, then Atlantic salmon may have been shifting their habitat use and spending more time taking refuge to reduce the costs of competition (Schluter 2000). Taking refuge in the rocky substrate could alter Atlantic salmon's morphology by limiting the development of their musculature associated with swimming (; Webb 1984, Kieffer 2010, Palstra and Planas 2011). This could happen through a reduced exposure to higher water velocities, which are known to induce streamlined, fusiform body shapes through exercise (Pakkasmaa and Piironen 2001), and less access to food (Currens et al. 1989, Pakkasmaa and Piironen 2001, Peres-Neto and Magnan 2004, Leavy and Bonner 2009). We did not detect differences in burst swimming speed between strains or treatments, however, this may be due the naiveté of hatchery-reared fish to predation risk from above (Álvarez and Nicieza 2003). We noted that most many individuals were unresponsive to stimuli from above and it took several attempts to initiate the burst swimming behaviour. Therefore we cannot draw any strong conclusions about the effects of interspecific competition on this mode of swimming.

2.5.3 Morphology and swimming performance

Morphology has an intricate relationship with function in fish (Blake 2004). The streamlined, energy efficient morphotype characteristic of salmonids is an adaptation to prolonged swimming but may vary in function of the life-histories and the physical environmental constraints imposed on different populations (Taylor and McPhail 1985). Here, we provided support that a correlation exists between critical swimming speed and a streamlined body shape but that this relationship varies as a function of the interspecific competitor present. Only Atlantic salmon in the control treatments

developed significantly streamlined body morphologies. This is even more apparent in the control treatments of Sebago salmon where critical swimming speed was not only significantly greater over all other treatments but was also highly correlated to a streamlined body shape. This may also be a result of their more elongated head, contributing to a more streamlined shape, when compared with the LaHave. Interestingly, Pakkasmaa and Piironen (2001) reported that juvenile brown trout (*Salmo trutta*) developed streamlined bodies when reared in fast flowing water but not juvenile Atlantic salmon which instead developed deeper bodies. Although they also reported that they were both longer and had more elongated heads than salmon reared in low water velocity, which could nonetheless be interpreted as a streamlined morphotype (Pakkasmaa and Piironen 2001).

Developing deeper bodies may be adaptive for individuals faced with interspecific competition (Grether et al. 2009) and may give them a competitive advantage in interactions with interspecific competitors (i.e. it may give the impression of having a larger body size, a common sign of dominance in fish (Huntingford et al. 1990, Ward 2006). This appears to be at the cost of swimming performance. We cannot, however, conclude that the deeper-bodied morphology gives a competitive advantage through burst swimming performance as burst swimming did not vary between treatments and was not correlated with morphology. This is likely due to the naiveté of hatchery-reared fish towards predation (Pakkasmaa and Piironen 2001, Álvarez and Nicieza 2003). Alternatively, interspecific interactions may be forcing Atlantic salmon into sub-optimal territories in the artificial streams. This may result in reduced access to resources and to faster-flowing water, a factor known to induce streamlined body shapes in salmonids (Finstad et al. 2011, Fu et al. 2013). This is plausible as these interspecific competitors have been shown to affect Atlantic salmon habitat use (Houde et al. 2015). Either way, the deeper-bodied morphotype, induced by the

presence of interspecific competition, led to a decrease in swimming performance which could have negative impacts on individual fitness in the wild. Juvenile Atlantic salmon prefer territories with faster water velocities (riffles) and fish with lower critical swimming speeds would not be able to hold this territory (Pakkasmaa and Piironen 2001, Armstrong et al. 2003).

2.5.4 Considerations for conservation

The changes in morphology induced by competition that we observed in individuals' lifetimes may eventually result in an ecological character shift of stocked populations in the wild when competitors are present (Schluter 2000). Competition produced two distinct morphotypes (fusiform or deep-bodied) which performed differently, and this could reflect differences in the amount of exercise and thus, development of musculature that individuals experienced (Johnston et al. 2011, Palstra and Planas 2011, Lailvaux and Husak 2014). In the wild, this induced shape change in the presence of interspecific competition may result in individuals that are mismatched with regard to their preferred habitat (fast flowing riffles which are associated with high levels of invertebrate drift) which require a greater swimming performance to exploit (Finstad et al. 2011). Stream flow strongly influences the spatiotemporal distribution of fish and consequently, morphology and swimming performance limit the territories that individuals can occupy (Peres-Neto and Magnan 2004, Leavy and Bonner 2009). In the wild, Atlantic salmon with deeper bodies and consequently poorer swimming performance could be marginalised to poorer quality habitats and forced to switch to lower quality resources rather than incur injury through competition (Milinski 1982, DeWitt et al. 1998). Deviation away from this optimal habitat might then result in decreased fitness (Sih et al. 1985). In order to increase the

fitness of Atlantic salmon in the wild and the success of stocking programs, interactions with competitors need to be minimised to ensure that morphology and swimming performance are optimised to the local environment (Diamond and Smitka 2005). This is particularly important in the case of Lake Ontario Atlantic salmon reintroductions which face competition from these non-native interspecific competitors. Information on factors that impede the establishment of a self-sustaining population of Atlantic salmon will aid in understanding the factors contributing to their successful reintroduction and re-establishment of a historical top aquatic predator in the Great Lakes.

CHAPTER III

ENVIRONMENTAL VARIATION INFLUENCES INTRASPECIFIC COMPETITION, INDIVIDUAL MORPHOLOGY AND GROWTH IN A HATCHERY-REARED FISH

3.1 Abstract

Hatchery-reared fish have lower fitness in the wild and display a number of maladapted traits when compared to their wild counterparts. Introducing environmental variability early in life may be a way to produce phenotypic diversity among individuals in a hatchery-reared population which may improve the success of these individuals in the wild. We experimentally manipulated the spatial distribution of resources and group density in juvenile Atlantic salmon, a highly territorial species. We tested whether growth and morphology differed as a function of the spatial distribution of resources and the number of competitors in a trial. The type and intensity of competition was expected to vary with respect to the costs and benefits of defending the resources and as a function of the size of the individual. We compared the growth and morphological change that individuals experienced across these treatments as well as relative to their particular social group. We found that these differences in the abiotic and biotic environments influenced the type and intensity of intraspecific competition. Both the spatial distribution of resources and fish density interacted significantly to influence morphological change and growth across treatments. Within social groups, relative growth and morphological change varied as a function of the competitive scenario imposed by the treatment. Both a mix of scramble and contest competitions were apparent but, contrary to our expectations, it

was the larger and not the smaller individuals which grew the least during the experiment. Furthermore, we found that morphological change did not result in lower growth. Together with our results suggest that morphological diversity and growth can change after a very short exposure to environmental variation. These changes in individual phenotypes created a diversity of foraging strategies that may be beneficial to otherwise uniformly reared hatchery fish that are released in the wild

3.2 Introduction

Phenotypic plasticity is an adaptive response in which a species can acclimate to environmental variation in space and time (Via and Lande 1985, Tonn et al. 2010). However, environmental variation can also constrain development as there are trade-offs with other life-history traits (DeWitt et al. 1998, Monaghan 2008). The abundance and spatial distribution of resources are some of the main sources of environmental variation capable of producing and maintaining phenotypic diversity in the wild (Ward et al. 2006, Roberts et al. 2011). Variation in traits that are linked with competitive ability among individuals in a population is an important driver of selection. Intense intraspecific competition for limited resources across a heterogeneous environment can pose a significant challenge to conservation authorities as managing the overlapping needs of multiple species is demanding (Fausch 1988, Grant and Guha 1993, Grand and Grant 1994, Ward et al. 2006). Moreover, understanding how different environments can influence growth and the phenotype of populations is essential in conservation management. This is particularly true of fisheries where there are challenges in balancing fish production and ecosystem conservation (Pitcher 2001, Worm et al. 2009). As such, conservation authorities need to understand how species targeted for reintroduction acquire and

process food, interact with conspecifics and move in complex environments (Brown and Day 2002).

Having a better understanding of the behavioural ecology of a population can aid in the success of a conservation program. Over the years there have been many theories as to how individuals can optimize their foraging behaviour in a heterogeneous environment (Milinski 1982, Milinski 1984). For instance, the ideal free distribution (IDF) hypothesis, explains how individuals of equal competitive ability could distribute themselves across resource patches of varying quality (Fretwell and Lucas 1970). It predicts that higher quality resource patches should contain more individuals than poorer patches. However, in natural environments, individuals vary in their competitive abilities, and competition for scarce resources rarely results in equal partitioning of the resources (Ward 2006). An alternative model, the ideal despotic distribution (IDD) model, assumes uneven competitive ability between individuals and predicts that dominant individuals will defend high-quality patches, excluding subordinates and leaving them with poorer quality patches. The extent of the dominant individual's territory depends on the trade-offs between the energetic costs and benefits associated with defending territories (Fretwell and Lucas 1970, Grant 1997, Milinski and Parker 1991b, Ward et al. 2006).

Intraspecific competition is influenced by the abundance and distribution of resources in space and time (Clutton-Brock and Harvey 1977, Isbell 1991) and individuals differ in their abilities to cope with environmental heterogeneity (Ward 2006, Dingemanse et al. 2013). Resources that are more spatially clumped may result in more contests while spatially dispersed resources may result in more scramble competition (Nicholson 1954, Rubenstein 1981b, a). If resources are dispersed, then

competitive interactions are less likely to happen and a relatively even partitioning of resources among individuals should occur (Van Schaik and Van Noordwijk 1988, Ward et al. 2006). Spatially clumped resources, on the other hand, are easier to defend, can be monopolized by dominant competitors, and result in more competitive interactions (Grant and Guha 1993, Bryant and Grant 1995, Koenig 2001). This also holds true for resources that are predictable in both space and in time (Grand and Grant 1994, Humphries et al. 1999b, Goldberg et al. 2001). The competitor to resource ratio also determines the prevailing type of competition observed and has consequences on the net gain of energy for all individuals in a population (Isbell 1991, Humphries et al. 1999a, Koenig 2001, Noël et al. 2005). The social dynamics imposed by the interaction between the abundance and distribution of resources, as well as the density of competitors per resource, can influence long-term population size (Van Schaik and Van Noordwijk 1988, Sibly et al. 2007).

Many species of fish develop different morphologies as a function of the environment in which they were reared (Norton et al. 1995, Peres-Neto 2004, Fraser et al. 2011, Hendry et al. 2011, Senay et al. 2015). Intraspecific competitors with different morphologies will necessarily exploit resources in different ways (Keast and Webb 1966, Norton et al. 1995, Wainwright and Richard 1995). Morphology influences competitive ability through its impact on an individual's hydrodynamics and swimming performance (Webb 1984, Blake 2004, Ward 2006). Aquaculture, however, can produce fish that are maladapted to natural habitats in a number of traits, as a result of environmental homogeneity. For example, salmonids raised in hatcheries develop different morphologies with less morphological variation than their wild counterparts and are generally weaker swimmers (Solem et al. 2006, Rouleau et al. 2010, Pulcini et al. 2013). Fish raised in hatcheries are also less efficient at foraging, defending territories and, responding appropriately to environmental variation (Metcalfe et al. 2003, Solem et al. 2006, Larsson et al. 2011).

This poor adaptation to natural environments may be one of the greatest impediments of using hatchery-reared fish for reintroductions. Taking advantage of salmonids' morphological plasticity (Imre et al. 2002, Hutchings 2007) could be a useful strategy in improving reintroductions after a long history of failed reintroductions (Coghlan et al. 2007, Crawford and Muir 2007, Homberger et al. 2014, Houde et al. 2015b).

While fisheries have strived towards creating genetic diversity among their populations, the loss of fitness is still a major obstacle to many conservation programs (Fraser 2008). Early exposure to environmental enrichment and variation may reduce maladaptive behaviour in salmonids (Neff et al. 2011, Roberts et al. 2011). Introducing environmental variation may improve response to predation (Dill and Fraser 1984, Lima and Dill 1990, Martel and Dill 1993, Martel 1996, Brown and Day 2002, Henderson and Letcher 2003), create a diversity of morphologies (Keeley and Grant 1995, Jacobson et al. 2015), influence growth patterns (Jacobson et al. 2015), improve foraging success (Brown and Laland 2002), and modulate agonistic interactions in territorial defense (Puckett and Dill 1984, Grant et al. 1998, Steingrímsson and Grant 1999, Dubois et al. 2003). Producing and managing phenotypic diversity, rather than simply selecting for large individuals within genetically diverse source populations, may better prepare source populations used for reintroductions and stocking for challenges imposed by the natural environment (Watters et al. 2003, Denoël and Winandy 2015, Houde et al. 2015b). Lake Ontario Atlantic salmon have yet to re-establish a self-sustaining population after extirpation despite over one hundred years of stocking initiatives. Recently two candidate replacement strains (LaHave and Sebago), each with similar genetic and ecological backgrounds to the original Lake Ontario population, have been selected as source populations for large scale reintroductions (Huntsman 1944, Netboy 1968, Parrish et al. 1998, Diamond and Smitka 2005).

In light of the challenges faced by naïve hatchery-reared fish that are introduced into heterogeneous environments, the goal of this study was to assess how different environments could influence intraspecific competition and result in differences in competitive ability (i.e. growth) between these two candidate strains of juvenile Atlantic salmon. To do this we experimentally varied the fish population density and the spatial distribution of resources in artificial streams and followed the development of individuals over the course of a week. We predicted that individual morphology and growth would change both across and within treatments. We hypothesized that larger individuals would be able to monopolize resources which were clumped when there were fewer competitors and would acquire more mass during the experiment. On the other hand, we expected that larger individuals would not be able to successfully defend resources when they were dispersed and the numbers of competitors were greater, which would result in fewer differences in overall growth in a trial. We also predicted that there would be a trade-off between overall growth and morphology. That is, gain in mass would differ between individuals developing streamlined morphologies vs. deeper bodied morphologies. Streamlined morphologies would be better suited to prolonged swimming, when resources were dispersed and the numbers of competitors were greater and deeper bodied morphologies, better suited for burst swimming, would prevail when resources were clumped and the numbers of competitors were lower. Diversity and plasticity in foraging which would be advantageous strategies and development may allow individuals to acclimate to their physical and social environments. Finally, we predicted that there would be a trade-off between growth and morphology in the context of territorial defence for limited resources. Muscle is expensive and developing and maintaining the muscle mass necessary for swimming performance is critical for all foraging strategies. A trade-off should occur if individuals divert resources away from overall growth towards morphological change (Metcalfe et al.

1989, Huntingford et al. 1990b, DeWitt et al. 1998, Blake 2004, Lailvaux and Husak 2014).

Scramble competition was predicted to prevail in treatments where resources are spatially dispersed and higher fish density per resource should reduce the amount of growth for all individuals. In this case, plotting gain in mass against dominance status (using initial mass as a proxy for dominance) should yield near horizontal slopes whereas the difference in elevation between slopes should differ according to group size with the low-density treatments gaining more mass overall compared to high-density treatments. Asymmetric contests between dominant and subordinate individuals were predicted to occur in spatially clumped resource treatments that could be monopolised by dominant individuals. These same individuals should experience greater growth relative to subordinates. If fish density increases in this contest scenario, the overall growth of all individuals should decrease. Plotting gain in mass against initial mass, in this case, should yield a negative slope with dominant individuals making a relatively larger gain in mass than smaller individuals. The presence of both differences in elevation and slope was predicted to indicate some combination of contest and scramble competition (Van Schaik and Van Noordwijk 1988, Koenig 2001).

3.3 Materials and methods

3.3.1 Subjects

We obtained a total of 300 (150 LaHave/ 150 Sebago) juvenile Atlantic salmon for this experiment. Of these, only 126 from each strain were used (n = 252) and the remaining individuals were kept in reserve for replacements. They were produced from reproductive adults at the OMNRF Codrington Fisheries Research Facility who were selected randomly in order to create 20 distinct half-sibling family blocks in a 2x2 factorial mating design (see Chapter 1). After fertilisation, the eggs from each separate cross were randomly allocated to the cells of two separate incubation stacks to control for block effects. Survival of the fertilised eggs was monitored three times a week until the latest date of hatching (March 4, 2013). Dead eggs were determined by visual inspection and removed from the trays as they occurred. Once the alevin had absorbed their yolk sacs and manual feeding began, up to 100 individuals (97 ± 1.2) from each full sibling cross were transported in May of 2013, from the incubation trays at Codrington and randomly allocated into separate 40 L family rearing tanks at the University of Windsor Great Lakes Fish and Research Centre in LaSalle, Ontario. Water quality (dissolved oxygen, pH, and temperature) was examined daily to ensure families were being held at optimal water conditions. In April of 2013, each tank was manually thinned down to 50 individuals in order to accommodate growth and limit density effects on the early growth of the fish. In July of 2013, 300 individuals from pure LaHave and Sebago families were pooled and transported to Concordia University's Loyola Campus in Montréal, Québec. They were subsequently housed at Concordia University's animal care facility, in four 133 L circular constant-flow tanks (flow at ~0.25m/s, temp. approx. 18-22°C varying daily) on a 12h light: 12h dark cycle (lights on at 9am) and fed a maintenance ration (3% total body weight) of dry EWOS salmon feed. Housing conditions and mortalities were monitored daily and feedings were provided by animal care staff at Concordia University, where the experiments were conducted.

3.3.2 Artificial streams

Experimental trials were conducted using four flow-through experimental stream channels under the same light regime. Each channel was lined with approximately 2.5cm of small, natural coloured aquarium gravel wherein nine terracotta flower pot trays, acting as resource patches embedded in the substrate. All artificial streams were surrounded by blackout curtains to ensure no disturbance from experimenters. Flow in each channel was held constant across all trials (0.25 m/s). Water temperature within the system (approximately 18-22°C) was controlled by the amount of dechlorinated city water into 2 re-circulating tanks (each fed a pair of interconnected channels) and by two industrial chillers (Frigid Units © Model D1-33, 4000 BTUs/hour). Water temperature was recorded daily and adjusted as required.

3.3.3 Experimental design

Feeding trials were conducted under a 2x2 factorial design for each strain testing two different resource distributions (dispersed and clumped) at each of two fish densities (low n=7 and high n=14) with 3 replicates per treatment (Fig. 1). Treatments were conducted four at a time from July 1 to August 30, 2013. Individuals were randomly assigned to each treatment and artificial stream. Each trial lasted one week.

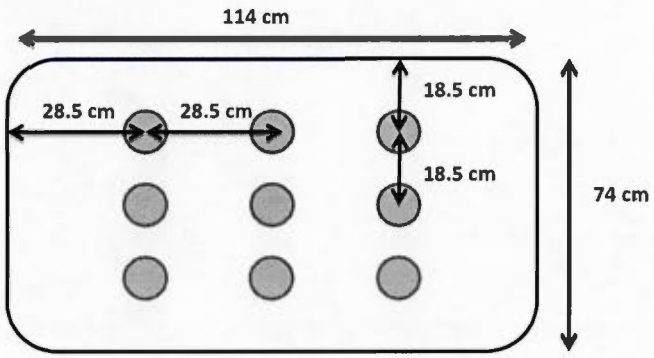

Figure 3.1 Artificial stream channel dimensions. There were four identical such stream channels used in this experiment. The substrate was natural coloured aquarium gravel and the terracotta dishes (orange circles) were embedded in the substrate so as to be flush. The dispersed resource distribution treatment divided the fish food evenly across the nine dishes while the food was only placed on the central dish in the clumped treatment. Fish densities were either high (n = 14) or low (n = 7).

The day before each experimental week, a random subset of individuals from each strain were taken from their holding tanks and lightly anaesthetized using a 1:10 clove oil ethanol solution (active agent: eugenol), weighed, photographed, and allowed to recover in cool oxygenated water. They were then placed in the stream channels according to the randomised design. The food (Commercial EWOS fish feed) was replenished and distributed according to the experimental design for the next five days (5% total body weight in order to encourage growth but promote competition. The food was evenly divided across the 9 patches (dispersed treatment) or concentrated in a single central patch (clumped treatment) (Brown & Brown 1993). This was done by immersing the food pellets in water, putting them in a medical syringe, and randomly depositing the food on the terracotta plates according to the randomised design. On Day 6, the food was not provided to ensure proper stomach evacuation for accurate weight measurements. On Day7, individuals were euthanised with an overdose of the clove oil solution after being weighed and photographed.

3.3.4 Data analyses

We tested how individual morphologies changed as a function of treatments. We used general Procrustes analysis generates Procrustes-aligned coordinates from 19 homologous landmarks (Figure 0.4) overlaid on the digital photograph of each individual (2 sets of landmarks per individual). These shape variables were then used to compare the morphology of each individual before and after the experiment. To determine whether an individual's shape changed in function of treatment we performed a Procrustes ANOVA with 9999 permutations to describe patterns of shape variation and co-variation for the set of Procrustes-aligned coordinates (Adams and Otarola-Castillo 2013, Adams et al. 2013). To test how shape changed across treatments we included before/after, as well as all possible interactions of density, resource distribution, and strain as fixed effects in the model. To visualise the differences in shape across treatments we used discriminant function analysis on the final shape coordinates using strain, density, and resource distribution as the grouping factors. The discriminant functions were then regressed on the corresponding shape coordinates using thin-plate-splines with the 'TPSreg' software to produce deformation grids (Rohlf 2006).

We compared how individuals grew across different environments, using three growth metrics calculated for each individual: 1) Individual growth, G_{ind}, calculated as the difference between $\log_{10}$ transformed final and initial masses (Noël et al. 2005). This described how individuals differed in growth across treatments; 2) Relative growth, G_{rel}, calculated as the difference between G_{ind} and the mean G_{ind} of the

treatment. This described how individuals varied in growth within treatments compared to their neighbours; and 3) Growth variance, G_{var}, calculated as the absolute value of G_{rel}. This metric was used to describe the magnitude of differences in growth trajectories between individuals within treatments. We used GLMMs to predict G_{ind} and G_{rel} using initial mass, density, and resource distribution as fixed effects and individual id nested within strain as random effects. Date and artificial stream used were also included as random effects. We also tested for a relationship between an individual's initial mass and G_{ind} using Pearson's product-moment correlation coefficients.

We determined whether there was a trade-off between growth and morphological plasticity by calculating the Euclidean distance between initial and final morphologies for each individual. This variable served as a proxy for the magnitude of morphological change experienced by each individual. We then calculated Pearson's product-moment correlation coefficients to assess whether a relationship existed between individual growth (G_{ind}) and growth variance (G_{var}) and, the magnitude of morphological change, for each strain and treatment.

GLMMs were performed using the R package nlme v. 3.1-120 (Pinheiro et al. 2006). Geometric morphometrics were done using the R package 'geomorph' v. 2.1.5 (Adams and Otarola-Castillo 2013). All statistical analyses were performed in R v.3.23 R Core Development Team (2016).

3.4 Results

Morphology changed significantly over the course of the week-long experiment. Using a repeated measures Procrustes MANOVA (n = 487, d.f. = 486) we found that the interaction between strain, density, and resource distribution significantly influenced morphology (Table 3.1). By plotting discriminant functions which separate morphological variation by strain, density and resource distribution we were able to visualise the differences in morphology across treatments (Figure 3.2). LaHave tended to have shallower bodies whereas Sebago tended towards larger heads and deeper bodies. Fish in the high-density treatments also tended towards larger heads and deeper bodies as well as deeper caudal peduncles. Fish in low-density treatments tended to have shallower bodies and more elongated heads as well as a more anterior attachment of the pectoral fin. Fish in the clumped treatments tended to have deep bodies and caudal peduncles while fish in the dispersed treatments tended to have larger heads relative to their bodies, a more anterior attachment of the pectoral fin, and narrower caudal peduncles (Figure 3.2).

Table 3.1 Results of Procrustes ANOVA on the Procrustes-aligned shape coordinates. A randomized residual permutation procedure with 9999 was used (n = 487, d.f. = 486).

	d.f.	SS	MS	F	Z	p-value
Density	1	0.004	0.004	2.70	2.40	0.0041
Resource Distribution	1	0.003	0.003	2.52	2.26	0.0059
Strain	1	0.012	0.012	8.14	7.29	<0.001
Initial *vs*. Final	1	0.007	0.007	4.88	4.46	<0.001
Density x Resource Distribution	1	0.002	0.002	1.35	1.25	0.17
Density x Strain	1	0.002	0.002	1.14	1.06	0.29
Resource Distribution x Strain	1	0.003	0.003	1.69	1.58	0.06
Density x Resource Distribution x Strain	1	0.003	0.003	2.21	2.04	0.02

The mean initial mass of individuals across all treatments and strains was 1.22 ± 0.48 g and the mean final mass was 1.28 ± 0.52 g. Fish in the high-density-dispersed treatment grew the most with 73% of individuals gaining mass. Only 48% of individuals in the high density-clumped treatment and 48% of individuals in the low-density-dispersed treatment gained mass. Few individuals (26%) grew in the low density-clumped treatment. Growth or loss of mass was slight over the course of the one week experiment but the degree to which individuals grew differed greatly across and within treatments, suggesting differences in competitive ability between individuals (Table 3.2).

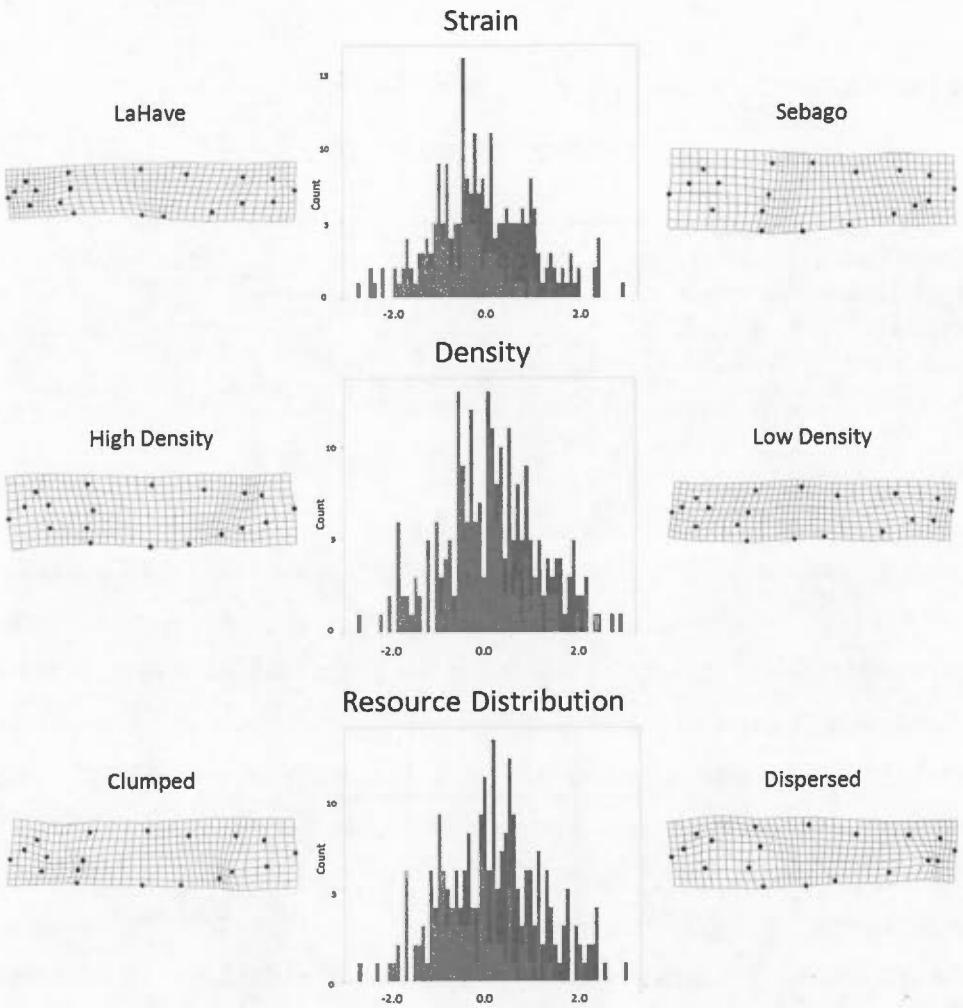

Figure 3.2 Histograms of the discriminant functions (x-axes) separating the final Procrustes-aligned coordinates by strain, fish density and resource distribution respectively. Deformation grids showing differences in morphology between groups were obtained are also shown.

Table 3.2 Mean individual growth G_{ind} per treatment.

Treatment	Strain	Mean G_{ind}	s.d.
High Density-Dispersed	LaHave	0.04	0.17
High Density-Clumped		0.03	0.16
Low Density-Dispersed		0.00	0.34
Low Density-Clumped		-0.04	0.06
High Density-Dispersed	Sebago	0.08	0.20
High Density-Clumped		0.07	0.33
Low Density-Dispersed		0.02	0.12
Low Density-Clumped		0.00	0.09

To test how growth varied across treatments we used a GLMM to predict growth using density and resource distribution as fixed effects and initial mass as a covariate. All fixed effects were set to fully interact as fish size is an important indicator of dominance in fish. There was a significant interaction between density and resource distribution (Table 3.3; Figure 3.3; Figure 3.4A). Fish in high-density treatments tended to have greater overall growth relative to fish in the low-density treatments. Greater individual growth was also observed in the dispersed treatments relative to the clumped treatments. Initial mass, density and resource distribution also significantly interacted to predict individual growth (Table 3.3). This suggests that the initial size of the individual is a good predictor of growth but is modulated by the environment. We tested the relationship between initial mass and individual growth and found a significant negative correlation ($r = -0.22$, $n = 470$, $p < 0.001$). Surprisingly, the largest individuals were the ones that grew the least and also tended to lose mass despite their presumed position in the social hierarchy.

To assess whether contest or scramble competition was more prevalent in each treatment we compared the slopes and elevations of individual growth plotted against

initial mass which served as a proxy for dominance status (Van Schaik and Van Noordwijk 1988, Koenig 2001). We observed differences in both slope and elevation across each treatment confirming the existence of intraspecific competition across our treatments; however, our results did not match our predictions (Table 3.3, Figure 3.3). Negative slopes were observed in the high density-clumped, high-density-dispersed and low-density-dispersed treatments indicating the prevalence of asymmetric contest competition. In contrast to our expectation, it was the smaller individuals (i.e. subordinates) that had greater relative growth instead of the larger individuals. A difference in the slope elevation between these treatments indicated a difference in their net gains of mass suggesting a mix of contest and scramble type competitions that varies with density. A near horizontal slope in the low density-clumped treatment is indicative of scramble competition as no single individual gains more mass than others (Figure 3.3).

Table 3.3 Results from GLMM used to predict individual growth (G_{ind}) across treatments. (n = 470, d.f. = 235)

Parameters	Value	S.E.	t-value	p-value
$Mass_i$	-0.14	0.04	-3.37	<0.001
Resource Distribution	-0.11	0.10	-1.17	0.24
Density	-0.26	0.10	-2.62	<0.01
$Mass_i$ x Resource Distribution	0.09	0.08	1.27	0.21
$Mass_i$ x Density	0.15	0.07	2.16	0.03
Resource Distribution x Density	0.31	0.15	2.06	0.04
$Mass_i$ x Resource Distribution x Density	-0.22	0.11	-1.99	0.04

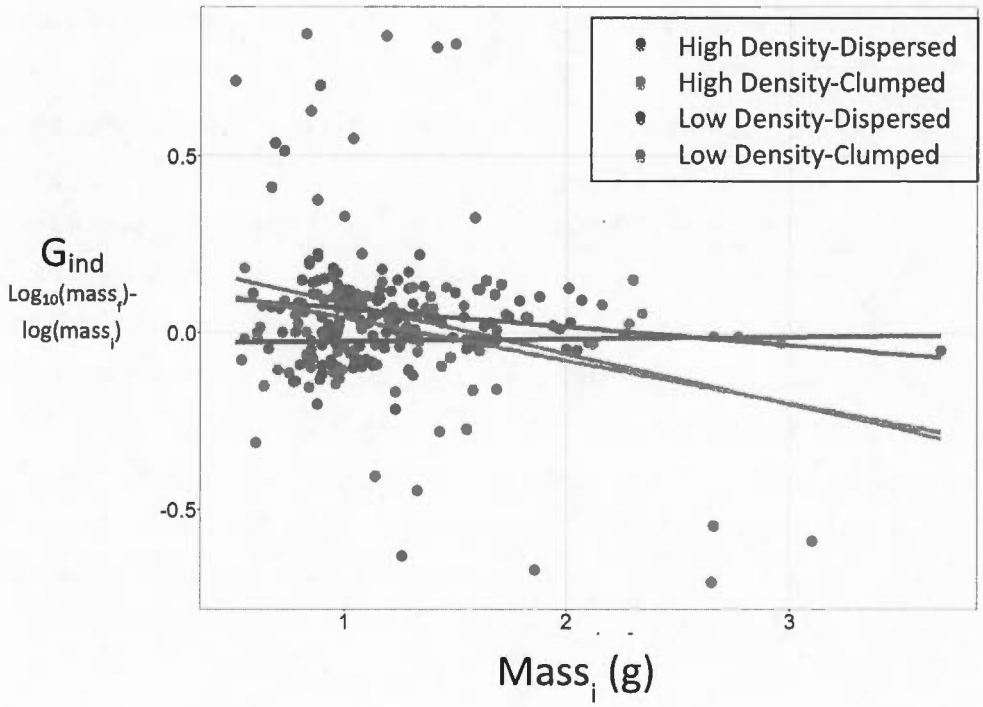

Figure 3.3 Individual growth G_{ind} plotted by initial mass.

To test how an individual's growth varied relative to other individuals within a treatment, G_{rel} was used as the response variable in a GLMM (Table 3.4). Relative growth within treatments varied similarly to individual growth across treatments. Initial mass, density and resource distribution interacted significantly to predict relative growth while an interaction between resource distribution and density alone did not significantly predict relative growth. By comparing the results across and within treatments we see that there is a complex interaction between the abiotic and biotic environment and that individuals respond differently to this variation. Some general patterns can, however, be teased apart. By examining the growth variance within treatments (i.e. the degree to which individuals gained or lost mass in a

treatment), we see that individuals in the low density-clumped and high-density-dispersed treatments had low growth variance (i.e. they grew relatively similarly). On the other hand, individuals in the high-density-clumped and low-density-dispersed treatments had greater variance in growth. The differences in growth suggest that there were differences in individual competitive abilities and these varied across environments (Figure 3.4B).

Table 3.4 Results from GLMM used to predict relative growth (G_{rel}) within treatments. (n = 470, d.f. = 235)

Parameters	Value	S.E.	t-value	p-value
$Mass_i$	-0.14	0.04	-3.01	<0.001
Resource Distribution	-0.13	0.10	-1.32	0.19
Density	-0.19	0.10	-1.94	0.05
$Mass_i$ x Resource Distribution	0.09	0.08	1.27	0.21
$Mass_i$ x Density	0.15	0.07	2.16	0.03
Resource Distribution x Density	0.29	0.15	1.92	0.06
$Mass_i$ x Resource Distribution x Density	-0.22	0.11	-1.99	0.04

Finally, we tested whether there was a trade-off between individual growth or growth variance, and the magnitude of morphological change an individual experienced during the course of the experiment. We found little evidence for a trade-off between growth and morphological change across all treatments and strains (Table 3.5). This means that even if fish changed their morphology it did not impact their growth. There was, however, some evidence for a negative correlation between growth variance and morphological change for Sebago in the high and low density-clumped treatments ($r = -0.36$, $p = 0.03$, $n = 470$, and $r = -0.39$, $p = 0.09$, $n = 470$ respectively).

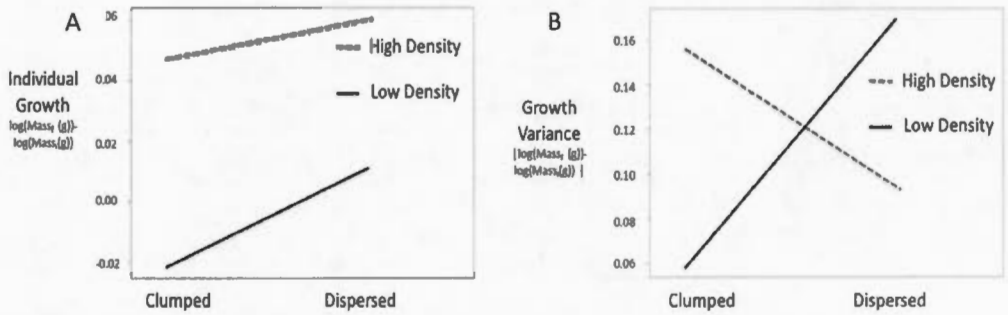

Figure 3.4 Interaction plots showing the effects of treatment on individual growth across treatments (A) and growth variance within treatments (B).

Table 3.5 Pearson product-moment correlation coefficients (r) used to assess the relationship between individual growth and growth variance and, morphological change. Morphological change was calculated as the Euclidean distance between the initial and final morphologies of each individual. Numbers in parentheses are the sample size.

	G_{ind}		G_{var}	
	r	p-value	r	p-value
LaHave High Density-Dispersed (42)	0.12	0.45	0.12	0.45
LaHave High Density-Clumped (38)	0.06	0.74	-0.11	0.51
LaHave Low Density-Dispersed (20)	-0.00	0.97	0.02	0.94
LaHave Low Density-Clumped (19)	-0.02	0.94	-0.18	0.46
Sebago High Density-Dispersed (42)	-0.11	0.51	-0.24	0.13
Sebago High Density-Clumped (35)	-0.12	0.50	-0.36	0.03
Sebago Low Density-Dispersed (19)	-0.06	0.80	-0.11	0.66
Sebago Low Density-Clumped (20)	-0.16	0.50	-0.39	0.09

3.5 Discussion

This study demonstrated that the morphology of juvenile Atlantic salmon is plastic and can change significantly within a very short period of time (a week, in this study). Patterns of morphological variation were induced by differences in the biotic (fish density), and abiotic (resource distribution) environments. The environment also significantly influenced individual growth across treatments as well as relative growth within treatments. Our results also support the prediction that resource distribution and group size interact to influence the type of competition observed in a system; however, we found that it was the largest individuals initially, that lost the most mass in these competitions. Finally, contrary to our expectations; we found little evidence for a trade-off between growth and morphological change. Together, the differences in morphology and growth found both across and within treatments, suggest that competitive ability is modulated not only by the environment but also by an individual's initial phenotype as well as the phenotypes of conspecifics (i.e. their social environment). The phenotypic plasticity displayed by both strains has important implications in the way hatcheries produce fish. It lends support to the idea that introducing environmental variation early in life can produce greater variation in fitness-related traits, and better prepare hatchery-reared fish for the diversity of niches available in natural settings. This also applies when determining optimal sites for reintroduction or stocking in which environmental heterogeneity and fish density should be taken into account.

3.5.1 Differences in morphology

We observed that different environments can produce significant differences in morphology after only one week of exposure. Although size is the usual metric used to predict competitive ability in fishes (Ward et al. 2006), differences in body shape can affect locomotion and influence the foraging strategy employed in territory defence contexts (McLaughlin et al. 1994, Ward et al. 2006). Indeed, small changes in morphology can lead to large differences in performance (Keast and Webb 1966, Webb 1984, Garland and Losos 1994, Koehl 1996). The greatest amount of morphological variation that we observed was in body and head depth, head length, caudal peduncle depth and the attachment of the pectoral fin. High density and dispersed resources tended to produce deeper bodies and heads. This may reflect a state of better nourishment (Currens et al. 1989). As predicted, a greater proportion of individuals grew in the high-density and dispersed resource treatments when compared to low-density and clumped treatments. Deeper-bodied fish are generally faster, can accelerate faster, and have a greater muscle mass than shallow bodied individuals (Domenici and Blake 1997, Domenici et al. 2008). Variation in body depth may also indicate muscle development, or lack thereof, due to differences in net gains in early growth (Currens et al. 1989). Head morphology varied in length and depth across treatments and may also have an impact on locomotion (Pakkasmaa et al. 1998, Blake 2004). Variation in head morphology can also influence the way in which individuals forage as well as affect antagonistic social interactions (Keast and Webb 1966, Pakkasmaa et al. 1998, Solem et al. 2006, Adams 2010). Variation in the relative attachment position of the pectoral fin also varied across treatments. Pectoral fins are particularly important for juvenile Atlantic salmon who use them as

hydrofoils to hold stationary positions on the substrate in fast flowing water (Arnold et al. 1991). Variation in this morphological feature may relate to differences in energy expenditure between individuals. Finally, while, Currens et al. (1989) found little variation in caudal peduncle morphology in a study on salmonids faced with different feeding regimes, we found a lot of variation in the depth and length of the caudal peduncle. The variation that we observe may be the result of an interaction between food availability, as well as the swimming demand imposed by the distribution of resources.

3.5.2 Growth across and within treatments

Growth across treatments, as well as relative growth in relation to individuals, within the same treatment, varied significantly as a function of an interaction between fish density, the spatial distribution of resources and one's initial mass. This is in contrast with Jacobson et al. (2015) who found no relationship with individual growth and initial mass in a similar study. In the present study, a greater proportion of individuals grew in the high-density-dispersed treatments whereas few individuals grew in the low-density-clumped treatments. There was also little difference in growth variance between the high-density-dispersed and low-density-clumped groups suggesting that either all individuals in a treatment gained a lot of mass, or very little, respectively. Our results are supported in part by a long-term study of stream-dwelling salmonids that found that the strongest effects of fish density on growth occurred at low densities, whereas growth declined at higher densities (Imre et al. 2010). Although we controlled for food abundance by giving it as a percentage of the total mass of fish per trial, its spatial distribution, and differences in the rates of depletion of each patch may have created local differences in food abundance. These differences could have

influenced the intensity of competition at each patch. For example, the intensity of competition was low when food was scarce or overabundant in a study observing the foraging tactics of convict cichlids (*Archocentrus nigrofasciatus*) as the costs of territorial defence outweighed the benefits (Puckett and Dill 1984, Treganza et al. 1996, Noël et al. 2005). Only intermediate amounts of food or spatially clumped patches produced intense competition among convict cichlids (Grant and Guha 1993, Grant et al. 2002). Our data support this idea as approximately half of the individuals in the high-density-clumped and low-density-dispersed treatments had positive growth and there was greater growth variance in these treatments implying asymmetric competitive ability. Fish with appropriate morphologies and foraging strategies were able to out-compete individuals who lacked those phenotypes.

Salmonids are among the few species to actively defend territories outside of a reproductive context (Keenleyside 1979). Their territories vary with their size and are also density dependent (Keeley and Grant 1995, Grant et al. 1998, Steingrímsson and Grant 1999, Imre et al. 2004). The boundaries of the territories are, however, fluid over time as the patchiness of resources in space and time varies greatly in their natural environment (Armstrong et al. 1999, Roy et al. 2013). This dynamic mosaic of territorial defence all but ensures intraspecific competition and asymmetric acquisition of resources. Dominant individuals can hold a virtual monopoly on resources once territories are acquired and the costs of subordination are large (Kvingedal and Einum 2011, Nislow et al. 2011).

It is, therefore, surprising that the largest individuals in our experiment grew the least across all treatments. The differences in elevations and slopes we observed when individual growth was plotted against initial mass suggest a mix of contest and

scramble type competition within treatments (Van Schaik and Van Noordwijk 1988, Koenig 2001). Different individuals may be employing different foraging strategies that are explained by factors other than density and the spatial distribution of resources. Larger fish may be using a contest strategy while all others are scrambling.

Behavioural traits associated with dominance may, in fact, precede developing a larger size (Huntingford et al. 1990a). For instance, aggressive and bold behaviour are known to predict future social status and growth in fish (Huntingford 1976, Metcalfe et al. 1989). There may also be a complex interaction between the environment and individual behaviour that influences foraging strategy (MacLean et al. 2000). For example, food abundance and competitor density modulate aggression in a territorial defence context for convict cichlids and rainbow trout (Noël et al. 2005, Toobaie and Grant 2013). Larger individuals may have been foregoing feeding in an active attempt to aggressively establish territories. Indeed it has been shown that dominant Atlantic salmon are less likely to feed in novel environments and there may actually be a decrease in growth rate initially as they attempt to establish a hierarchy (Grant 1997, Sakakura and Tsukamoto 1998, Cutts et al. 2002, Martin-Smith and Armstrong 2002, Harwood 2003). Moreover, poorer competitors increase their feeding rates when they perceive increased interference competition (Dill and Fraser 1984, MacLean et al. 2000). A long-term study would be needed to further investigate these dynamic growth patterns.

3.5.4 Morphological plasticity and growth

We found little evidence for a trade-off between morphological change and growth in our study. In a study similar to our own, Jacobson et al. (2015) found that morphological variation in juvenile rainbow trout was related to relative growth but did not vary as a function of fish density or the spatial distribution of resources, and was unrelated to the initial mass or length of the individual. They found that the individuals that grew the most also developed deeper heads and bodies and larger caudal fins. Although most fishes show similar shape patterns (Wainwright and Richard 1995, Blake 2004) it is difficult to generalize about variation in morphology and its relationship to growth among salmonid species as their morphological response differs across environments (Swain and Holtby 1989, Pakkasmaa et al. 1998, Pakkasmaa and Piironen 2001, Peres-Neto and Magnan 2004). Complex environments impose many different selective pressures which may influence resource allocation or different types of morphological plasticity (Sundström et al. 2004, Irschick et al. 2008). Also in contrast with our study, a trade-off between morphological plasticity and growth rates was demonstrated both experimentally and in the field for Eurasian perch (*Perca fluviatilis*). Morphological plasticity only occurred in individuals with greater growth rates and thus may only be possible when a surplus of resources is available (Olsson et al. 2006, 2007). Since our study lasted only a week, and resources were limited to promote intraspecific competition, a clear relationship between growth and morphological plasticity may not have had the time to be established.

Growth rate often trades off with a number of other life history traits. For instance, a faster growth rate is associated with increased mortality (Mangel and Stamps 2001,

Biro et al. 2006), decreased longevity (Metcalfe and Monaghan 2003), and decreased swimming performance (Álvarez and Metcalfe 2007, Criscuolo et al. 2011). Elevated growth rates are also associated with riskier behaviour in dominant fish which can negatively impact fitness (Huntingford and Torricelli 1993, Harwood 2003, Stamps 2007). Indeed, plasticity in fitness-related traits may be constrained due to the high energetic costs in changing (DeWitt et al. 1998, Miner et al. 2005).

3.5.5 Implications for reintroductions

Re-establishing viable populations of extirpated species in the wild is notoriously difficult and the causes of failure are not well understood (Fischer and Lindenmayer 2000). A major hurdle to overcome is the prevalence of maladapted phenotypes produced in domesticated captive source populations. There has been a call to introduce environmental variation and simulate ecological processes during early life in artificial breeding programs. This increases the diversity of phenotypes in a source population (Watters et al. 2003, Neff et al. 2011, Roberts et al. 2011) and may allow individuals to occupy a greater variety of niches once released in the wild (Ackermann and Doebeli 2004, Conrad et al. 2011, Houde et al. 2015b). Salmonids, in particular, can undergo rapid evolution and locally adapt to environmental variation once established, though they need the phenotypic diversity to succeed in a new environment before selection can take place (Stockwell et al. 2003, Fraser et al. 2011). In this study, we showed that juvenile Atlantic salmon could develop significantly different morphologies and growth patterns after only a week-long exposure to complex environments. The type and intensity of competition observed were also associated with growth and morphology indicating within group differences in competitive ability and foraging strategy. Our data support the idea that

introducing environmental variation early in life may benefit a number of fitness-related traits and may contribute to the success of reintroduction programs.

CHAPTER IV

BEHAVIOURAL AND MORPHOLOGICAL PLASTICITY INTERACT ACROSS DIFFERENT ENVIRONMENTS TO INFLUENCE GROWTH

4.1 Abstract

Individual behaviour plays a central role in mediating the relationship between morphology and fitness across a heterogeneous environment, but this paradigm has never been tested in full. Activity, boldness, and aggressiveness are correlated in individuals and are linked with dominance and higher growth rates in many species. Intraspecific competition in juvenile Atlantic salmon is driven by density-dependent interactions and the spatial distribution of resources due to the territorial nature of their foraging tactics. Plasticity in behaviour and morphology may reduce the costs of competition for limited resources as it would create a diversity of foraging tactics among individuals in a population. This study tested whether the spatial distribution of resources and the density of competitors interacted to influence individual behaviour and morphology and how this could affect growth. To do this, we tested individual activity, boldness, and aggressiveness before and after being placed in artificial streams which differed in fish density and spatial distribution of resources. We found that individual behaviour was not consistent within individuals but that certain behaviours were favoured in different treatments. We also found that change in individual behaviour could predict relative growth. Finally, we found that while morphology and behaviour were not initially related, a significant relationship developed after being placed in these heterogeneous competitive environments. To the best of our knowledge, this is the first study to establish a link between

morphology, growth, and behaviour. Understanding correlations between these traits can provide useful insight as to why certain behaviours are favoured in different environments.

4.2 Introduction

The ecomorphological paradigm has been used as a framework to evaluate how variation in morphology leads to variation in performance, and how this leads to differences in fitness among individuals within populations (Arnold 1983) (Figure 0.1). Put another way, form and function interact to produce differences in the competitive ability of individuals in a population, ultimately determining how individuals exploit resources (Ward et al. 2006). This framework has since been expanded to incorporate how environmental variation and individual differences in behaviour can modulate the relationships between form and function (Figure 0.2) (Garland and Losos 1994, Lailvaux and Husak 2014). Animal personalities are associated with a number of important life-history traits and have a strong influence on population and group dynamics (Miner et al. 2005, Réale et al. 2010). One should, therefore, expect individual behaviour to vary as a function of environmental variation (both physical and social), but many species, across a wide variety of taxa, have been shown to be limited in their behavioural plasticity (DeWitt et al. 1998, Sih et al. 2004, Conrad et al. 2011). This relationship may be context dependent, and be contingent upon the relative costs and benefits of plasticity that individuals incur when exposed to strong selective pressure (e.g. competition) (Fausch 1998).

The nature and intensity of competition are influenced by the distribution of resources, and individuals differ in their abilities to cope with spatial variation and temporal fluctuations in the environment (Milinski and Parker 1991a, Ward 2006, Ward et al. 2006, Dingemanse et al. 2013). Resources that are more spatially clumped may result in more contests while spatially dispersed resources may result in more scramble competition (Rubenstein 1981b, a). Indeed, it is well recognised that if resources are evenly dispersed, then competitive interactions are less likely to occur than if the resources are clumped. In the former case, there would be a more even partitioning of resources amongst individuals (Ward et al. 2006). Consequently, clumped resources, that are easier to defend, can be monopolised by relatively superior competitors (Grant and Guha 1993, Bryant and Grant 1995). This also holds true for resources that are predictable in both space and time (Grand and Grant 1994, Humphries et al. 1999b, Goldberg et al. 2001). As such, plasticity in behavioural and morphological traits would appear adaptive across these different contexts as individuals can reduce the costs of competition by modifying their foraging strategies and developing morphologies better suited to their environments.

Competitive ability, the capacity to acquire and defend resources, must be treated as a context dependent attribute because it depends on the number of other individuals in the group and the traits that they bare. The social environment thus contributes to the type and intensity of interactions, (Milinski 1988, Ruzzante and Doyle 1993, Humphries et al. 1999a), and can potentially determine individual differences in behaviour that reduce competition through repeated encounters (Magnhagen and Staffan 2004, Bergmüller and Taborsky 2010, Ward 2011, Keiser et al. 2014, Laskowski and Bell 2014). Although poorly understood, this relationship may be species and context dependent (i.e. an interaction between the abiotic and social environment (Humphries et al. 1999b, 2000, Miner et al. 2005). It follows that

populations in which individuals vary in their behavioural traits important to foraging will have some individuals outperforming others in certain contexts and that particular behaviours may be more or less important in these different contexts (Dingemanse et al. 2004, Réale et al. 2010). Behavioural and morphological plasticity is a potential way to reduce the costs of competition. Weaker competitors (e.g. smaller, shyer individuals) could adopt an alternative foraging strategy that increases their feeding rate under increased interference competition (Dill and Fraser 1984). Similarly, by modifying aspects of their morphology, individuals could be able to exploit resources differently and improve their foraging success (Webb 1984, Pough and Taigen 1990, Koehl 1996, Chivers et al. 2007). However, the costs incurred in phenotypic modification are such that non-plastic individuals (i.e. those that are consistent in their behaviour and do not allocate their resources to developing a morphology better suited to the environment) may do equally well, compared to plastic individuals, in a competitive social group (Wolf et al. 2007, Wolf and Weissing 2010). The variable magnitude of these phenotypic changes would lead to differences in group dynamics, depending on the environment, and could range from contests where a single strong competitor could monopolize resources, to scramble competition where the costs of defending a territory are too great (Treganza et al. 1996, Noël et al. 2005). Importantly, the interaction between an individual's phenotype with those of the social groups in a heterogeneous environment can produce and maintain strong selective pressures on a population through time (Dingemanse et al. 2010, Dingemanse and Réale 2013). These genetic by environment interactions have given rise to the theory of animal personality.

Animal personalities are more consistent across contexts and over time than previously supposed (Dingemanse and Réale 2013). Individuals often differ in their relative activity, boldness, aggressiveness, and exploration with respect to their neighbours (Réale et al. 2007, Conrad et al. 2011), Conrad et al 2011). These

correlations of behaviours within individuals are called behavioural syndromes (Koolhaas et al. 1999, Sih et al. 2004, Réale et al. 2007, Réale et al. 2010). Individuals showing high levels of activity, boldness and aggression are also usually at a competitive advantage and often have a higher social status than individuals on the other side of the spectrum (Réale et al. 2010). Behavioural syndromes also appear to be reinforced or restructured when the population in question is exposed to some form of selection (e.g. predation or competition) suggesting adaptive plasticity (Bell and Sih 2007, Blanchet et al. 2008, Dingemanse and Réale 2013).

While many studies have looked at how certain behavioural traits are adaptive (Carrere and Maestripieri 2013), few have experimentally manipulated the social or physical environment to evaluate whether particular personalities were favoured in different environments or how they relate to morphology in determining resource acquisition and related fitness consequences. Both Lakowski and Bell (2013), and Castanheira et al. (2013) sought to test for behavioural consistency in individuals across different social and environmental contexts (using three-spine stickleback (*Gasterosteus aculeatus)* and Gilt-head sunbream (*Sparus aurata)* respectively). Borcherding and Magnhagen (2008) observed that both behaviour and morphology were influenced by food availability in Eurasian perch. Jacobson et al. (2015) compared growth and morphology patterns across different environments using brook trout and Harrison et al. (2015) and Losos (1990) observed how limb and tail length in lizards correlated with habitat use and locomotive behaviour. Despite these results, we still lack a full picture of the context dependent relationship between competitive ability, and morphological and behavioural plasticity (Garland and Losos 1994, Melville 2002). In particular, while morphological differences are well studied across species and populations (Peres-Neto 2004, Kusche et al. 2014, Senay et al. 2015), we know relatively little of what influences morphological variation within populations.

Fishes are good models to study behaviour (Conrad et al 2011) and several species have been extensively used to study variation in behaviour such as guppies, sticklebacks, zebrafish, cichlids and salmonids (Biro and Stamps 2008, Conrad et al. 2011, Toms and Echevarria 2014). In fish, variation in size is an important predictor of fitness. Larger fish are generally better foragers, more aggressive, bold and active and tend to easily monopolise resources (Grant et al. 2002, Ward 2006). The behavioural ecology of juvenile Atlantic salmon, in particular, has been very well documented (Nislow et al. 2011), though the gaps in knowledge mentioned above persist. While optimal territory size models predict a decrease in territory size with increasing food abundance (Milinski 1982, Milinski and Parker 1991a, Ward 2006), this may not hold true in the case of juvenile Atlantic salmon due to their relatively high natural densities and strong territorial defense (Steingrímsson and Grant 1999, Nislow et al. 2011). In fact, their territory size may be more contingent on population density and individual size rather than the distribution and quality of resources (Martel 1996, Imre et al. 2010, Forseth et al. 2011). Although it is accepted that juvenile Atlantic salmon actively defend contiguous territories at higher densities through displaying, chasing and biting (Keenleyside 1979, Nislow et al. 2011, Toms and Echevarria 2014), studies suggest that the complexity of their movement patterns and general activity is greater than previously thought (Armstrong et al. 1999, Berland et al. 2004, Ovidio et al. 2007, Einum et al. 2011). Despite having strong sedentary tendencies (Nislow et al. 2011), juvenile Atlantic salmon have large overlapping home ranges and periodically switch from a sedentary state to highly mobile states depending on fluctuations in the environment (Armstrong et al. 1999, Steingrímsson and Grant 2003, Roy et al. 2013). This plasticity in their behaviours may thus be adaptive in a heterogeneous landscape composed of different individuals.

We tested how individual behaviour was affected by the physical and social environment. We hypothesized that there would be consistent differences between individuals across the different treatments. Furthermore, we hypothesized that activity, boldness, aggressiveness would be correlated within individuals and that individual morphology would have a specific relationship with these behaviours. Finally, we hypothesized that the associations between behaviour and morphology would differ across treatments and would lead to different growth patterns across these same treatments. To answer these questions, we experimentally manipulated the spatial distribution of resources and the group density of juvenile Atlantic salmon in artificial streams which mimicked the natural substrate and flow they encounter in the wild. We also recorded each individual's behaviour and morphology before and after the experiment to evaluate how the different treatments influenced their behaviour and how this related to growth. The spatial distribution of resources and population density can influence individual behaviour through repeated competitive interactions (Bergmüller and Taborsky 2010, Laskowski and Bell 2014). If we find a significant relationship between growth, morphology, and behaviour that differs across different complex environments, then we will gain valuable insight in how to manage specific populations, with specific phenotypes, in different complex environments. We would be able to make more informed decisions in when, where, how to stock individuals in different environments.

4.2 Materials and methods

4.2.1 Subjects

We obtained a total of 300 (150 LaHave/ 150 Sebago) juvenile Atlantic for this experiment (a subset of the subjects from Chapter 3 of this dissertation). Of these, only 134 individuals from each strain were used (n = 168) to fit with the experimental design and the remaining individuals were kept in reserve for replacements. The fish were produced from reproductive adults at the OMNRF Codrington Fisheries Research Facility (44.18.05°N, 78.29.40°W) who were selected haphazardly in order to create 20 distinct half-sibling family blocks in a 2x2 factorial mating design. After fertilisation, the eggs from each separate cross were randomly allocated to the cells of two separate incubation stacks to control for block effects. Survival of the fertilised eggs was monitored three times a week until the latest date of hatching (March 4, 2013). Dead eggs were determined by visual inspection and removed from the trays as they occurred. Once the alevin had absorbed their yolk sacs and manual feeding began, up to 100 individuals (97 ± 1.2) from each full sibling cross were transported in May of 2013, from the incubation trays at Codrington and randomly allocated into separate 40 L family rearing tanks at the University of Windsor Great Lakes Fish and Research Centre in LaSalle, Ontario. The facility is equipped with a scaled down recirculation system to ensure that the water quality in all the tanks is similar, not unlike those found at the provincial Atlantic salmon hatchery in Normandale, Ontario. Water dissolved oxygen, pH, and temperature were examined daily to ensure families were being held in optimal water conditions. In April of 2013, each tank was manually thinned down to 50 individuals in order to accommodate growth and minimise density effects on the early growth of the fish. In July of 2013, 300 individuals from pure LaHave and Sebago families were pooled and transported to Concordia University in Montréal, Canada. They were subsequently housed at Concordia University's animal care facility, in four 133 L circular constant-flow tanks (flow at ~0.25m/s, temp. approx. 18-22°C varying daily) on a 12h light: 12h dark cycle (lights on at 9am) and fed a maintenance ration (3% total body weight) of dry EWOS salmon feed. Housing conditions were monitored daily and feedings were

provided by animal care staff at Concordia University, where the experiments were conducted.

4.2.2 Artificial streams

Experimental trials were conducted using four flow-through experimental stream channels. Each channel was lined with approximately 2.5 cm of small natural coloured aquarium gravel wherein nine terracotta flower pot trays, acting as resource patches, were embedded in the gravel. Commercial food pellets were deposited on top of each tray using a medicinal syringe to ensure that the pellets did not float. Flow in each channel was held constant across all trials (0.25 m/s). Water temperature within the system (~ 18-22°C) was controlled by the amount of dechlorinated city water entering into 2 re-circulating tanks (each fed a pair of interconnected channels) and by two industrial chillers (Frigid Units © Model D1-33, 4000 BTUs/hour). Water temperature was recorded daily and adjusted as required.

4.2.3 Experimental design

Trials were conducted under a 2x2 factorial design for each strain and two different resource distributions (dispersed and clumped) for each of the two densities (low n=7 and high n=14) with 2 replicates per treatment (Fig. 1). Trials were conducted four at a time in four separate stream channels from July 1 to August 30, 2013. Individuals

were randomly assigned to treatments and treatments were randomly assigned to stream channels. Each trial lasted 7 days.

A day before being randomly chosen for an experimental treatment, food was not provided to all individuals in the holding tanks to ensure proper stomach evacuation to ensure accurate mass measures (Currens et al. 1989). On Day 1 of each experimental week, individuals were randomly selected from the holding tanks to fill the required number necessary for each treatment. To measure individual behaviours, each individual was placed in a 20 L (35 cm x 30 cm) opaque plastic container which served as an open field. It was filled with 10 cm of fresh water at 18°C and fish were left to acclimate in a small sectioned off part of the container for 5 minutes. The individual behaviour assessment was performed prior to as well as after experimentation in the stream channels (Day 1 and Day 7). A mirror was fixed at the opposite end of each container to simulate the presence of an unknown conspecific of equal competitive ability (i.e. the same size) (Balzarini et al. 2014). Each individual's behaviour was recorded for 10 minutes with an independent overhead CCD bullet camera connected to a surveillance system set up in a parallel circuit (Geovision Inc.). Every individual from a given trial was recorded simultaneously after being randomly assigned to one of the aforementioned fourteen plastic containers. Each individual was recorded for 10 minutes to quantify three behavioural traits, namely: activity, boldness and aggressiveness. This was done twice for each individual, once before being placed in the experimental treatment and once after. Activity was calculated as the total distance travelled (cm) within the open field during the 10 minutes of the trial. Boldness was calculated as the Log_{10} transformed latency (s) to approach within 5 cm (approx. one body length) of the mirror (perceived conspecific competitor). Aggressiveness was calculated as the Log_{10} transformed cumulative duration (s) that each individual spent within 5 cm of the mirror (i.e. in proximity to a perceived

competitor) (Toms and Echevarria 2014). Juvenile salmonids are highly aggressive and defend territories actively (Nislow et al. 2011). Any proximity to conspecific can be safely assumed to be aggressive in nature; however, we did visually inspect each recording for the characteristic lateral displays that define aggressive behaviour in fishes (Balzarini et al. 2014, Toms and Echevarria 2014). We also calculated the differences between final and initial activity, boldness and aggressiveness (Δ Activity, Δ Boldness and Δ Aggressiveness, respectively), as a metric of behavioural plasticity to be used in our analysis of relative growth (see below).

Following the initial behavioural measurement each individual was lightly anaesthetized using a 1:10 clove oil ethanol solution (active agent: eugenol), weighed and photographed before being placed in the stream channels according to the randomised design. Food (dry commercial EWOS fish feed) was given and replenished each day and distributed according to the experimental design for the next five days (5% total body weight, in order to encourage growth but promote competition and evenly divided across the 9 patches (dispersed treatment) or concentrated in a single central patch (clumped treatment), (Brown & Brown 1993). This was done by immersing the food pellets in water, putting them in a medical syringe, and randomly depositing the food on the terracotta plates according to the randomised design. On Day 6, food was not provided to ensure proper stomach evacuation for accurate weight measurements after the experiment. Post experiment behavioural trials proceeded in the same manner as described above. After all behavioural measures were completed; fish were euthanised with an overdose of clove oil, weighed on a digital scale, and photographed for later individual identification and geometric morphometric analysis.

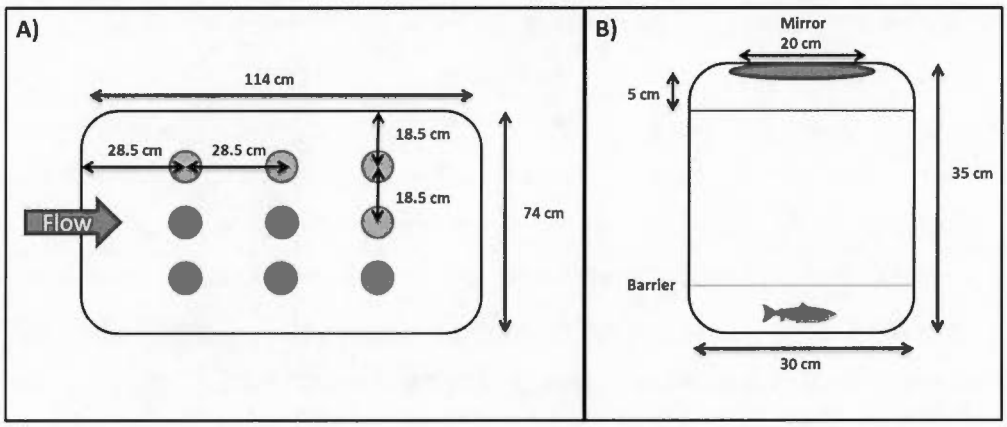

Figure 4.1 Layouts of stream channel and open field design: A) Stream channel dimensions and distribution of resource patches (terracotta dishes represented as orange circles). The dispersed resource distribution treatment divided food evenly across the nine dishes, while in the clumped treatment the food was only placed on the central dish. B) A total of 14 20L open fields filled with 10cm of water were used in the behavioural trials and all individuals were filmed for 10 minutes from an overhead camera simultaneously for each trial.

4.2.4 Data analyses

General Procrustes analysis was used to generate Procrustes-aligned coordinates from 19 homologous landmarks (Figure 0.4) overlaid on the photograph of each individual (2 sets of landmarks per individual: initial and final). These were then used to compare the morphology of each individual before and after the experiment. To determine whether individual shape changed as a function of treatment we performed a Procrustes MANOVA with 9999 permutations (Adams and Otarola-Castillo 2013) to describe patterns of shape variation and co-variation for the set of Procrustes-aligned coordinates. We included before/after, as well as all interactions between density, resource distribution and strain as fixed effects in the model. To visualise the

differences in shape across treatments we used discriminant function analysis on the final shape coordinates using treatments (fish density x resource distribution) as the grouping factor. The discriminant functions were then regressed on the shape coordinates using thin-plate-splines with the 'TPSreg' software to produce mesh warp grids (Rohlf 2006). In order to assess the relationship between shape and behaviour, we used two-block partial least squares with 9999 permutations to test the association between the Procrustes-aligned coordinates and each of the three behaviours (Rohlf and Corti 2000) both before and after the experiment.

To establish how consistent measured behavioural traits were within individuals, we quantified the proportion of the total variation that could be attributed to variation among individuals versus variation within individuals. This was estimated with the R package 'ICC' version 2.3.0 (Sokal and Rohlf 1995, Wolak et al. 2012). We then compared the correlation between behaviours, within individuals, before and after the experiment, using Spearman's rank correlation coefficient (rho). To further explore the correlation between the behaviours among individuals, 5 principal components analyses were calculated using the correlation matrix (one PCA for all treatments confounded before the experiment, and four separate PCAs for individuals separated by treatment after the experiment). This allowed us to compare the correlation structure between the behaviours before and after the experiment as well as to estimate whether and how treatments altered these correlations.

To determine the extent to which the physical and social environment (resource distribution and fish density respectively) could affect an individual's behaviour we used generalised linear mixed models (GLMMs) in a repeated measures design for each of the behaviour metrics. Fish density, strain, and resource distribution were

included as fixed effects and individual ID nested within trial were included as random effects. Interactions among all fixed effects were estimated. Date and specific stream channel used for a trial were not significant and were not included as random effects in the model.

Growth was used as an indirect measure of competitive ability and as a correlate of fitness (Conrad et al. 2011). Three growth metrics were calculated for each individual and used as dependent variables within all analysis: 1) Individual growth, G_{ind}, calculated as the difference between $\log_{10}$ transformed final and initial mass (Noël et al. 2005); 2) Relative growth, G_{rel}, calculated as the difference between G_{ind} and the mean growth of the trial in which the individual participated; and 3) Growth variance, G_{var}, calculated as the absolute value of G_{rel}. We used mixed models to determine how G_{ind} and G_{var} varied across treatments (spatial distribution of resources and fish density) using fish ID nested within strain as a random effect.

Next, we tested to what extent an individual's change in behaviour, in a given treatment, could predict its relative growth (G_{rel}) (i.e. how well an individual could grow relative to its neighbours in a given trial). Once again GLMMs were used and, included fish density and resource distribution as fully interacting fixed effects and, strain and individual id as random effects. We tested three models (one for each behavior), whereby individual change in behaviour (Δ = final value for a behaviour – initial value for a behaviour) and initial body mass were included as covariates (Δ Activity, Δ Boldness and Δ Aggressiveness, respectively).

GLMMs were performed using the R package nlme v. 3.1-120 (Pinheiro et al. 2006). Geometric morphometrics were performed using the R package 'geomorph' v. 2.1.5 (Adams and Otarola-Castillo 2013). All statistical analyses were performed in R v.3.23 R Core Development Team (2016). All behavioural measures were analysed with Ethovision XT 9 tracking software.

4.3 Results

4.3.1 Differences in morphology

Individual shape changed significantly as a function of resource distribution, density and strain (Table 4.1). The first two discriminant functions describing variation in final morphology by resource distribution and density (henceforth: DF1 and DF2) described 56% and 30% of the total variation in morphology respectively. By regressing DF1 and DF2 on the Procrustes-aligned shape coordinates using thin-plate-splines to produce warp grids we were able to visualise the differences in morphology produced by varying the fish population density and the spatial distribution of resources (Figure 4.1 B). The greatest variation we observed was in head angle, length and depth, as well as body and caudal peduncle depth. Along the DF1 axis, we observed differences in head length and pectoral fin attachment location. Along the DF2 axis, we observed differences in head length and depth as well as variation in the overall size of the head with respect to the rest of the body. We also observed variation in body depth and attachment of the pectoral fin attachment position. DF1 distinguished between the high-density-clumped, low-density-clumped and high-density-dispersed treatments, while DF2 separated

treatments between the low-density-dispersed treatment and all other treatments (Figure 4.1 A).

Table 4.1 Results of a Procrustes ANOVA (n = 156; d.f. = 311) with 9999 permutations and a residual randomization procedure to test how morphology changed as a function of strain, density and resource distribution from before to after the experiment.

Factors	F	Effect size (Z)	P - value
Before vs. After	5.35	4.66	< 0.001
Density	3.42	3.05	< 0.001
Resource distribution	3.25	3.02	< 0.001
Strain	7.25	6.47	< 0.001
Density x Resource distribution	2.87	2.69	< 0.001
Density x Strain	1.16	1.08	0.28
Resource distribution x Strain	0.92	0.87	0.48
Density x Resource Distribution x Strain	2.00	1.89	0.02

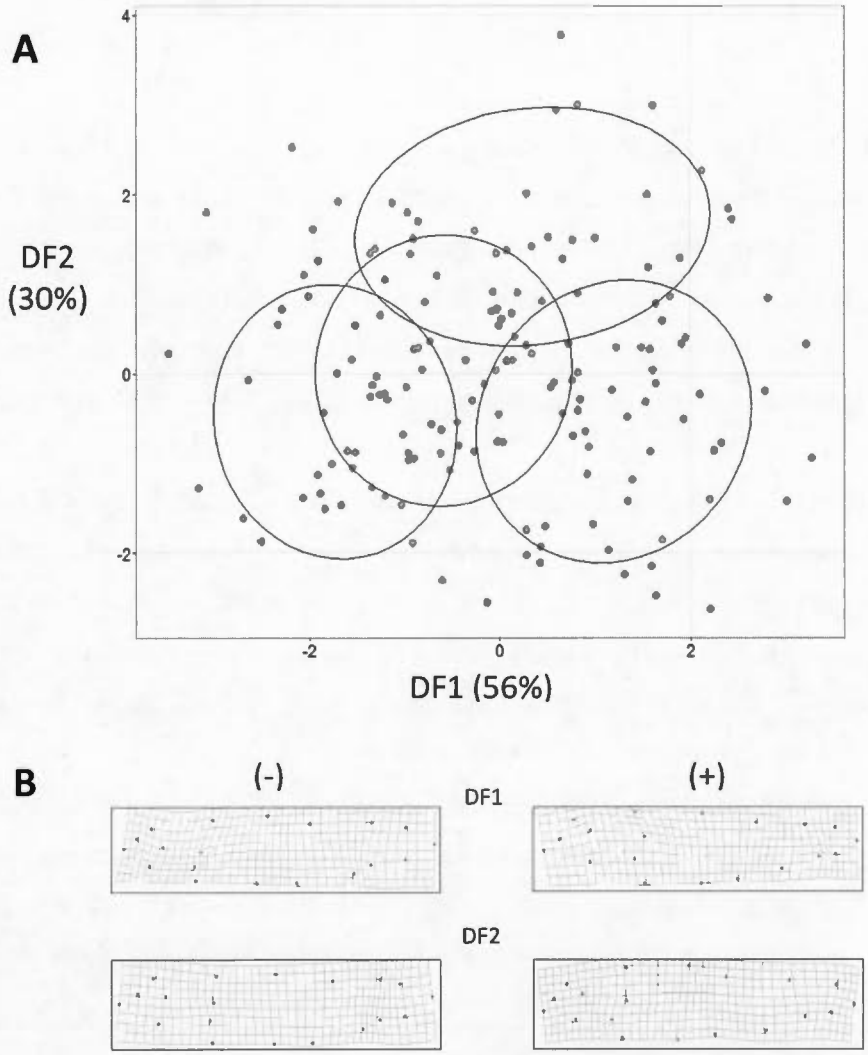

Figure 4.2 A) Axes as a function of density and resource distribution A), as the deformation grids associated with the extreme values of those functions B). A) Each point represents one individual. Colours represent the different treatments: (red = High Density-Clumped; blue= Low Density-Clumped; green = High Density-Dispersed; violet = Low Density-Dispersed). 95% confidence ellipsoids group treatments. B) Deformation grids describing morphological differences obtained by regressing DF1 and DF2 on the shape coordinates using thin-plate-splines.

4.3.2 Behaviour

Overall, there was a 43% decrease in activity across all treatments from initial activity measures. The overall differences between final and initial boldness and aggressiveness were less extreme (Table 4.2). Before the trials, all three behaviours were positively correlated within individuals (Table 4.2), but there was an uncoupling of behaviours after the experiment. Activity and aggressiveness were no longer significantly correlated within individuals, though they still tended to associate positively. Overall individual behaviours showed little consistency as the variance within individuals was far greater than that among individuals (Table 4.2). We further examined the correlation structure of these behaviours before and after the experiment by using principal components analysis. A scree plot showing the eigenvalues for each component (Figure 4.4 D) shows differences in how each treatment influenced the three behaviours. High variance in the first components indicates a greater degree of correlation between the behaviours. When compared with the initial variance (first component explaining 60% of the variance), we see that individuals from the high-density-dispersed, high-density-clumped and, low-density-dispersed treatments are less correlated to each other (first components explaining 52%, 44% and 43% of the variance respectively). Only individuals from the low-density-clumped treatment (first component explaining 64% of the variance) show greater correlation structure than what was initially measured.

Table 4.2 Pair-wise Spearman rank correlation coefficients between behaviours before and after the experiment. (*) denotes $P < 0.05$. Intra-class correlation (ICC) coefficients indicating the repeatability (i.e. consistency) of each behaviour within an individual, calculated as the ratio between the variance between individuals with the variance within an individual for each behaviour.

Correlation	Initial	Final
Activity-Boldness	0.34*	0.39*
Activity- Aggressiveness	0.28*	0.15
Boldness-Aggressiveness	0.41*	0.52*

Behaviour	ICC	Variance Within	Variance Among
Activity	0.04	243153.30	10640.69
Boldness	0.02	2672.13	51.25
Aggressiveness	0.00	4315.97	12.00

As behaviours were not consistent within individuals, we tested whether the manipulation of fish density and the spatial distribution of resources could predict the average individual behaviour after experimentation. GLMMs of all the initial behaviours indicated that they did not differ between strains and that the randomization in the experimental design prevented any significant patterns in behaviours from occurring before the experiment had begun (Figure 4.3). We did, nonetheless, observe that the treatments significantly influenced behaviour (Figure 4.3; Table 4.3). Final activity was influenced by fish density (GLMM: $t = -2.62$, $p < 0.01$) with the greatest levels of activity observed in the high-density treatments. Activity was also influenced by an interaction between strain and resource distribution (GLMM: $t = 2.72$, $p < 0.01$; Table 4.3). Treatment and strain did not predict the average boldness of individuals, though there was a trend towards greater levels of boldness in individuals in the low density-clumped treatments and shyer individuals in the high density-clumped treatment (Table 4.4, Figure 4.3). Average

aggressiveness was, as with activity, significantly influenced by fish density (GLMM: $t = -2.00$, $p = 0.04$) with greater amounts of aggression on average observed in the high-density treatments and a trend towards less aggressive behaviour in the low density-clumped treatment (Figure 4.3).

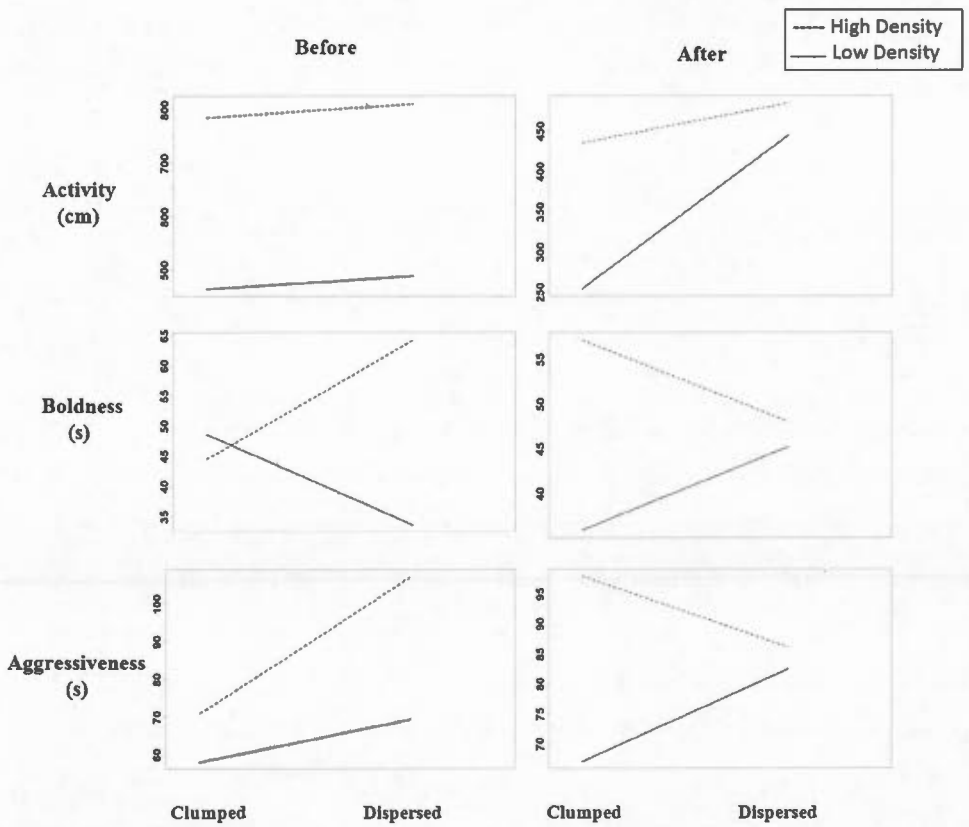

Figure 4.3 Interaction plots showing the influence of resource distribution and fish density on average activity, boldness and aggressiveness before and after the experiment.

Table 4.3 The t-values from GLMMs (n = 156; d.f. = 148) describing the effects of treatment on final individual behaviour.

Factors	Final Behaviours		
	Activity	Boldness	Aggressiveness
Strain	-2.90**	-0.44	0.16
Resource distribution	-1.44	-1.06	-0.85
Density	-2.62**	-1.12	-2.00*
Resource distribution x Density	1.82	0.85	1.53
Strain x Resource distribution	2.72**	0.63	0.30
Strain x Density	1.48	-0.13	0.91
Strain x Resource distribution x Density	-1.36	-0.16	-1.00

* P-value < 0.05
** P-value < 0.01
*** P-value < 0.001

To examine the relationship between individual morphology and behaviour, we used two-block partial least squares to test for correlations between the Procrustes-aligned coordinates and each behaviour prior to, and following, exposure to the different treatments (Table 4.4). Before the experiment, morphology and behaviour were not correlated with one another; though, after the week-long experiment, significant correlations between morphology, activity, aggressiveness, but not boldness, were observed.

Table 4.4 Results of two-block partial least squares (PLS) correlation with 9999 permutations, testing the association between the Procrustes-aligned coordinates (shape) with each of the three behaviours, before and after the experiment.

	Initial		Final	
	PLS - Correlation	*P* – value	PLS - Correlation	*P* - value
Activity	0.34	0.05	0.37	0.02
Boldness	0.30	0.24	0.24	0.81
Aggressiveness	0.25	0.61	0.39	0.01

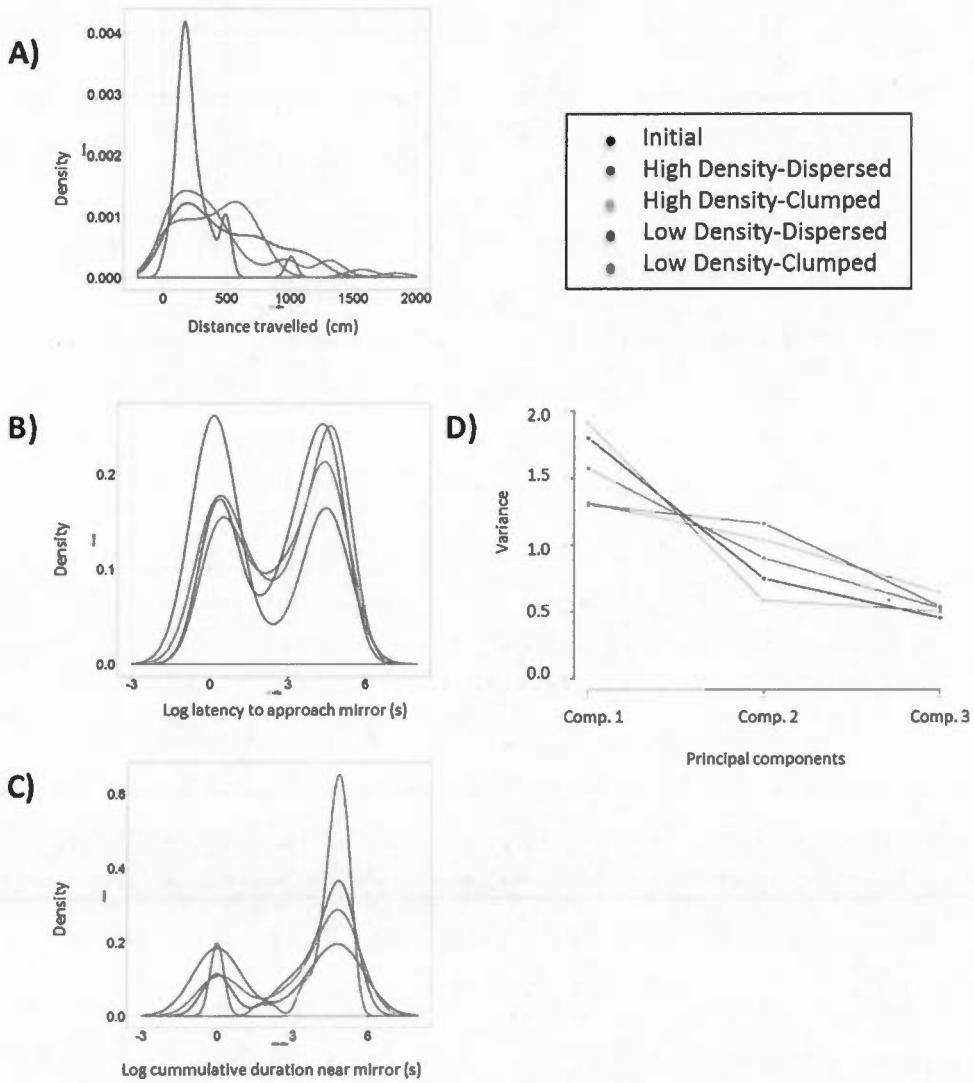

Figure 4.4 Density plots (A-C) showing the distribution of final behaviours and a scree-plot D) of the principal component analysis. A) Activity, B) Boldness and, C) Aggressiveness plotted by treatment. D) The eigenvalues associated with the principal components of the final behaviours, obtained using the correlation matrix.

We observed that the high-density-clumped treatment had a greater proportion of less active individuals, while the activity levels across other treatments were similar. A greater proportion of individuals in the low-density-clumped treatment were also bolder; though, we did discern a clear shy-bold axis across all treatments. We also observed a bimodal distribution of aggressive-docile individuals across all treatments; however, aggression was more prevalent in high-density-dispersed treatments (Figure 4.4 A-C).

4.3.3 Growth

Relative growth (G_{rel}) was significantly influenced by their change in behaviour, the spatial distribution of resources and, fish density (Table 4.5). There were a greater proportion of individuals with positive relative growth in the high density and dispersed treatments. A lower proportion of individuals had positive relative growth in the low density-clumped treatments regardless of the initial mass of the individual. There was also a tendency for the initially largest individuals in the high density-clumped and low density dispersed treatments to have lost mass (Figure 4.6, Table 4.5).

Table 4.5 The t-values from GLMMs (n = 156; d.f. = 139) regarding the effect of change (Δ) in a given behaviour and its interaction with the environment on relative growth (G_{rel}). The behaviours listed are to indicate which behavioural covariate was used in the model.

	Behaviours		
Factors	Activity	Boldness	Aggressiveness
$Mass_i$	-4.39***	-4.89***	-4.44***
Δ Behaviour	-1.72	-1.19	-2.49*
Resource distribution	-1.99*	-2.62**	-4.42*
Density	-2.18*	-2.70**	-2.59*
Resource distribution x Fish density	2.30*	2.98**	2.87**
$Mass_i$ x Δ Behaviour	2.06*	1.58	2.75**
$Mass_i$ x Resource distribution x Density	-2.29*	-2.84**	-2.86**

* P-value < 0.05
** P-value < 0.01
*** P-value < 0.001

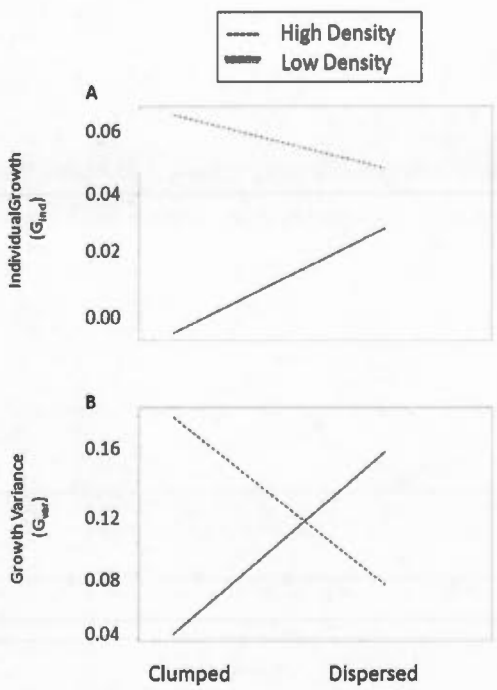

Figure 4.5 Interaction plots showing A) the mean individual growth (G_{ind}) across treatments and B) the mean growth variance (G_{var}) within treatments.

A greater proportion of individuals gained mass in high-density treatments in contrast to low-density treatments. Similarly, a greater proportion of individuals gained mass in clumped rather than dispersed treatments (Figure 4.5A, 4.6). Growth variance, which is defined by how similarly individuals in each treatment grew relative to each other (Figure 4.5B) was greater for individuals in the hig- density-clumped and low-density-dispersed treatments. There were greater differences in how individuals grew (i.e. lower G_{var}) in the low density-clumped and high-density-dispersed treatments.

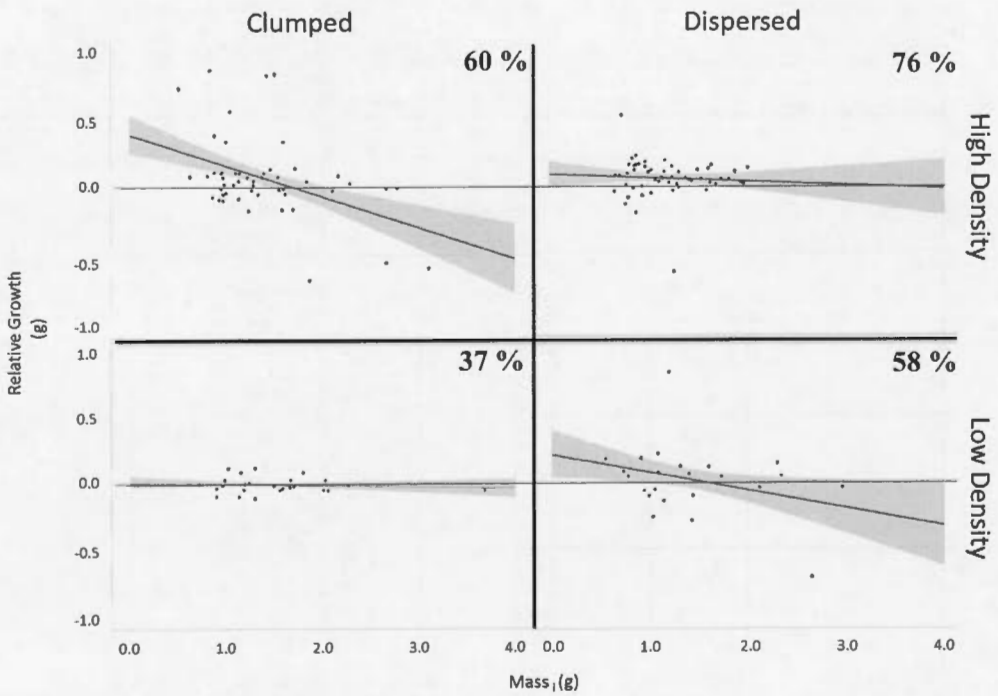

Figure 4.6 Plot of relative growth (G_{rel}) by initial mass sorted by treatment (see Table 5). Regression line (blue) with confidence intervals. The proportion of individuals in treatment with positive growth (above the red line) indicated in top right corner of each cell. Corresponds with data in Table 4.4.

4.4 Discussion

The goal of this study was to determine whether competitive ability was favoured by an individual's plasticity in behaviour across different competitive scenarios. We also tested if individual behaviours were consistent across different competitive contexts and how variation in morphology and behaviour were related. We established that relative growth (i.e. competitive ability) was significantly influenced by an individual's behavioural plasticity and was modulated by the spatial distribution of resources as well as the social environment. We also found that individuals did not have consistent behaviours across treatments and that fish density and resource distribution could significantly influence individual behaviour. Finally, we also found that while there was no relationship between individual behaviour and morphology initially, a relationship did develop after individuals were placed in a highly competitive scenario. To the best of our knowledge, this is the first time that any study has made direct links between individual morphology, behaviour and relative growth within an ecomorphological framework.

4.4.1 Differences in morphology

We found that the spatial distribution of resources interacted with fish density to produce different morphologies. A difference in morphology, in fishes, has a direct impact on locomotion and foraging strategy. Competition limits access to resources and can create maladapted morphologies (Currens et al. 1989). Individuals in the low density-clumped treatments had deeper heads, bodies and caudal peduncle as well a more anterior attachment of the pectoral fin which is indicative of musculature

developed for greater burst swimming ability (Blake 2004). This morphology should be adaptive as greater burst swimming ability may allow quick access to a clumped resource in a contest against a dominant individual which would actively attempt to chase others away from its territory. On the other hand, individuals in high-density dispersed-treatment tended towards longer heads relative to their body and a shallower more streamlined body shape. This is indicative of a greater capacity for prolonged swimming, which would be adaptive in moving across patches. Relative to the other treatments, individuals from the low-density-dispersed treatments tended towards shallower heads and bodies, a more anterior attachment of the pectoral fin, a shorter mouth and a narrower and shorter caudal peduncle. In contrast, Jacobson et al. (2015) found that variation in morphology was related to relative growth but did not vary as a function of fish density or the spatial distribution of resources in rainbow trout and was unrelated to initial mass or length of the individual.

4.4.2 Morphology and behaviour

Morphology was not initially related to any behaviour but was correlated to activity and aggressiveness following the experiment. This suggests that behaviour and morphology were linked in their response to fish density and the spatial distribution of resources. Swimming performance and foraging behaviour are intricately linked and this may limit morphological change and the development of alternative foraging strategies (Koehl 1996, Blake 2004). Indeed, differences in morphology can limit or facilitate aggression between individuals. For example, larger and more robust skulls and mouths were linked to greater aggression between individuals in both frogs and lizards (Relyea 2000, Adams 2010). Harrison et al. (2015) and Losos (1990) also found that lizard limb length and foot pad morphology constrained populations and

species to particular habitats and limited their range of locomotive behaviours and, suggested that populations reduced the costs of competition by exploiting different niches. Swain and Holtby (1989) also found that morphology and behaviour were correlated in a juvenile salmonid and that aggressive behaviours were greater in stream-dwelling individuals than in lake dwelling individuals. Juvenile salmonids living in lakes, which tend to shoal together, had more streamlined morphologies (shallower bodies and more posteriorly placed pectoral fins). In contrast, McLaughlin et al (1994) found that activity and morphology were not correlated in juvenile brook trout but that activity and foraging behaviour did determine habitat use. Borcherding and Magnhagen (2008) raised an interesting question and found that food availability affected both the morphology and behaviour of juvenile perch but that this may be due to malnourishment and the state of the individual in question. This, they argued would alter their active risk-taking behaviours (Currens et al. 1989) but they failed to take individual variation in behaviours into account during their study which was a central goal of our own study. Nonetheless, we found no relation between boldness and morphology in our study. Taken together, this lends credence to the idea that morphology and behaviour are correlated and that the strength of this correlation is favoured differently across environments.

4.4.3 Behavioural plasticity and growth

Contrary to expectations that individuals would be relatively consistent in their behaviours before and after experimental conditions (Sih et al. 2004, Bell et al. 2009), behaviours within individuals were not repeatable. Low repeatability in a given behaviour indicates that variation within individuals is greater than the variation among individuals. This suggested that the variation was a result of the environment

(Boake 1989, Bell et al. 2009). While the number of times an individual is measured should not affect the repeatability of a behaviour (Bell et al. 2009), there is nonetheless the risk that an individual, through habituation, may decrease their activity and exploration in an open field test (Martin and Réale 2008). The idea that the environment generates behavioural plasticity in individuals is consistent with our results where we see that both fish density and the spatial distribution of resources have the capacity to alter the average behaviour of the group depending on the treatment. Moreover, we observed that certain behaviour types are more frequent in certain situations than in others (Dingemanse et al. 2004, Réale et al. 2010). If the experiment were to continue over a longer period of time, we might observe that dominant individual would start to have positive growth after establishing their territory through repeated agonistic interactions (Johnsson and Akerman 1998, Bergmüller and Taborsky 2010). This plasticity in behaviour among competing individuals may be adaptive in the short term as they establish territories and a dominance hierarchy (Ward et al. 2006).

We observed that activity, boldness, and aggressiveness were correlated between individuals before the experiment. In fishes, study on behaviour has been biased towards boldness and aggression (Bell and Stamps 2004, Salonen and Peuhkuri 2006); however, positive correlations between boldness, exploration, activity, and aggression have all been documented across a wide number of fish species, particularly salmonids (Huntingford 1976, Øverli et al. 2004, Ward et al. 2004, Wilson and Stevens 2005, Øverli et al. 2006, Salonen and Peuhkuri 2006, Wilson and McLaughlin 2007). After experimentation there was a change in the behavioural syndrome and aggressiveness was no longer significantly correlated with activity or boldness (though it still tended towards a positive association). Similarly, Blanchet et al. (2008) found that behavioural syndromes and individual consistency in behaviour

in juvenile Atlantic salmon were disrupted when an interspecific competitor (rainbow trout) was present. The correlation structure observed between the measured behavioural traits depended on fish density and the spatial distribution of habitats and thus on the type and intensity of competition between individuals. We predicted that a strong contest competition would occur in the low density-clumped treatment, and we observed that behaviours were the most correlated in this treatment compared to the other treatments. This suggests that strong personalities are advantageous in this situation. We also predicted that the other treatments (i.e. high density or dispersed resources) would result in an equal partitioning of resources between individuals through a scramble competition. In these treatments, we observed a weaker correlation between the behaviours which suggests that a mix of foraging strategies may be more advantageous. This may depend on the composition of behaviours in the treatment as Magnhagen (2007) found that boldness and exploration in juvenile perch were only correlated when the behaviours of other group members were accounted for.

While Blanchet (2008) found no effect of either interspecific competition or predatory cues on the growth rate of Atlantic salmon we found that intraspecific competition across different environments produced significant differences in individual growth and variance. Our results were similar to those of Jacobson et al (2015) in that we found that an interaction between fish density and the spatial distribution of resources produced differences in individual growth and variance in growth among individuals. Lower individual growth paired with low growth variance in the low density-clumped treatments suggested that individuals grew similarly. This suggests a mix of scramble and contest competition, with larger individuals foregoing feeding in order to establish a territory, and smaller subordinate individuals scrambling for resources. As a result, individuals behaved and grew similarly on

average. Greater variance in growth in the high-density-clumped and low-density-dispersed treatments should be indicative of greater differences in competitive abilities between individuals. When initial mass was taken into account, we saw that the largest fish were losing weight relative to smaller individuals. Overall a greater number of individuals had positive relative growth in all treatments except for the low density-clumped treatment. We think that larger individuals may have foregone feeding in an active attempt to aggressively establish territories. Indeed, dominant Atlantic salmon are less likely to feed in novel environments and there may actually be a decrease in growth rate initially as they attempt to establish a hierarchy (Grant 1997, Sakakura and Tsukamoto 1998, Cutts et al. 2002, Martin-Smith and Armstrong 2002, Harwood 2003). Moreover, poorer competitors may increase their feeding rates when they perceive increased interference competition (Dill and Fraser 1984, MacLean et al. 2000).

Finally, we showed that the change in an individual's behaviour, as a function of its initial mass significantly influenced relative growth and that this varied with fish density and the spatial distribution of resources. A Larger size might, however, be the result of dominance in the social hierarchy rather than the other way around (Huntingford et al. 1990a) suggesting that an individual's personality can predict future social status and growth (Huntingford 1976, Metcalfe et al. 1989). In fact, the costs of being dominant in a novel environment can actually decrease a dominant individual's growth rate initially (Grant 1997, Sakakura and Tsukamoto 1998, Martin-Smith and Armstrong 2002, Harwood 2003).

In the wild, juvenile Atlantic salmon are mostly sedentary on the short term but can switch to a highly mobile state and engage in seemingly unprovoked aggression. This

may be because food availability in patches of running water is highly variable and individuals need to keep track of the relative quality of adjacent habitat patches (Keeley and Grant 1995, Martin-Smith and Armstrong 2002, Maclean et al. 2005). Aggression, activity, and boldness thus may have a larger effect on competitive ability in Atlantic salmon as opposed to just size (Metcalfe et al. 1989, Huntingford et al. 1990a, Jacobson et al. 2015). Indeed, these three behaviours have been linked to greater growth rate and food intake across many different species (Biro and Stamps 2008, Réale et al. 2010). We are not aware of any studies which have evaluated how individual behaviour varies across different habitat patches and how it might relate to morphology and growth in a natural setting. It would, therefore, be important to investigate how individual behaviours vary in the wild. Understanding the dynamic relationship between individual variation in behaviour, morphology, and growth and how it can vary across environments should be addressed in future ecomorphological studies.

CONCLUSION

The goal of my dissertation was to use the ecomorphological framework proposed by Arnold (1983) and Garland and Losos (1994) to test for known and unknown relationships between morphology, swimming performance, growth, individual behaviour, and competition across different complex environments. I combined field work and laboratory experiments to show that variation in morphology can be plastic within an individuals lifetime and that it takes very little time for a developmental trajectory to change. This had direct impacts on growth, a proxy for fitness, as well as a number of other fitness related traits. Each chapter explored different facets of this paradigm. I was able to make ecological inferences from morphological patterns by establishing clear correlations between morphology and ecology. I also established functional relationships between morphology and ecology as they were mediated by the behaviour and performance of the individuals as well as their interactions with interspecific competitors. Care was also taken to put the principles of ecomorphology and put them in a conservation context. The goal of future studies will be to provide further empirical evidence of these interactions and apply them to different species and taxa. This dissertation also provides a valuable tool to conservation authorities and biologists, particularly to those interested in fishes.

In summary, the main results of Chapter 1 were twofold. First, morphology but not genetic effects significantly influenced the swimming performance of Atlantic salmon parr. Furthermore, despite the high propensity of local adaptation in salmonids, two different populations of Atlantic salmon and their reciprocal hybrids did not differ in their swimming performance when reared in a similar environment. Second, individuals matched their morphologies to particular microhabitat features when

released in the wild. Chapter 2 focussed on how interspecific competition could influence morphology and swimming performance. This phenomenon has received little attention until now. Non-native salmonids, which are stocked in the Great Lakes, were found to have a significant impact on Atlantic salmon morphology and swimming performance. The nature of the mechanism which induces morphological differentiation and which affects an individual's resulting swimming performance remain unclear although we can hypothesize that might be due to both a shift in habitat use, as well as an inducible defense mediated through chemical alarm cues. In Chapter 3, relative growth and morphology were found to vary across different group densities and spatial distributions of resources. While the type and intensity of intraspecific competition were known to influence growth, its impact on morphology has not been seriously considered until now. Finally, in Chapter 4, individuals were found to change their behaviour as a function of the spatial distribution of resources and group density. This change in behaviour predicted relative growth within treatments and suggested that individuals may have modified their activity, boldness and aggression to employ different foraging strategies. This could reduce the costs of competition. Furthermore, morphology and behaviour were found to be correlated after a short exposure to these different competitive scenarios. While relationships between morphology and behaviour have been observed between locally adapted populations, this is was the first study to intentionally induce and test for a correlation between morphological and behavioural change.

I was able to expand upon the existing ecomorphological paradigm by exploring new relationships between morphology and swimming performance. I estimated the genetic component to swimming performance and found that it was not as important as morphology. I had hypothesized that there would be a significant genetic contribution to swimming performance, however I found none. Instead, I found that

individual morphology was sufficient in predicting swimming performance, with more fusiform individuals having greater critical swimming speeds. This relationship was further corroborated from my experiment on interspecific competition where I once again found a strong relationship between morphology and swimming performance that varied depending on the presence of different interspecific competitors. While I found no difference in the critical swimming speeds of LaHave, Sebago, or their reciprocal hybrids in Chapter 1, I did find that if left to develop over a longer period of time, the critical swimming speeds of those two strains differed across different contexts. Environmental variation would therefore appear to be a strong developmental influence on morphology and swimming performance. As I had established a clear relationship between morphology and swimming performance in Chapters 1 and 2, it is clear that the divergent morphologies developed in Chapters 3 and 4 will have significant impacts on swimming performance which will in turn influence foraging ecology and fitness. This will, of course, vary as a function of the abiotic environment and the social dynamics of the group.

The relationship between swimming performance and morphology has clear implications for conservation management. It implies that if fish are all reared in the same simple homogeneous environment, then they may not develop sufficient morphological variation to disperse and occupy habitats in natural streams. This idea is supported by the fact that there were clear significant differences in morphology across streams in Chapter 1, as well as across stream sections. Furthermore, individual morphologies significantly associated to specific microhabitat variables. Individuals might not only be sorting according to their phenotypes but might also be developing plastically when reared in even slightly different environments. This non-random dispersal could have profound impacts on the success of hatchery assisted stocking and reintroduction programs as hatchery-reared fish are known to have an

entire suite of maladapted traits and poor survival when released in the wild. In Chapters 3 and 4, I found that individual morphological trajectories could diverge within the space of a week. It is also clear is that stocking juveniles in habitats occupied by non-native salmonids could have a negative impact on their performance and may severely hinder the successful implantation of Atlantic salmon in the wild. Chapters 3 and 4 demonstrate that differences in morphology and competitive ability among individuals in a population may promote different foraging strategies and the occupation of a greater diversity of niches in the wild by hatchery-reared fish. Chapter 4 also shows that individuals with certain behavioural correlations might be favoured in certain environments. Together, these results imply that phenotypic sorting, plasticity, and selection interact together in determining where we will find individuals in the wild and which individuals will have a competitive advantage. Care should thus be taken to account not only for individual differences but producing genetically and phenotypically diverse individuals. Introducing more varied abiotic and biotic habitats for hatchery-reared fish may be a way to maximise survival in the wild as streams are spatially and temporally complex environments.

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